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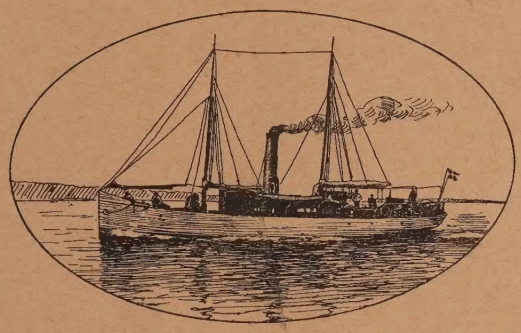

XXII.

1914.

By

C. G. Joh. Petersen,
Ph. D., L. L. D.
Director.

Copenhagen.
Centraltrykkeriet.
1915.

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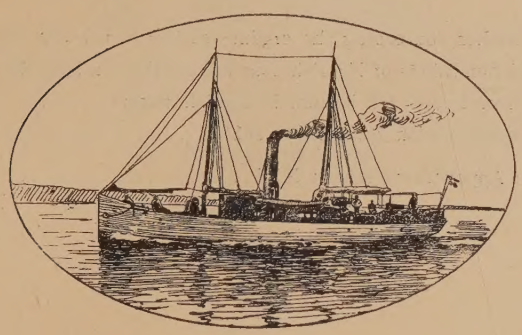

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Studies concerning the organic matter of the Sea Bottom.

By

P. Boysen Jensen.

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I. Origin of the organic matter of the sea bottom.

I. **Introduction.** As far back as 1890, in the Report of the Danish Biological Station No. I for that year, C. G. Joh. Petersen expressed the idea that the abundance of fish on our coasts was chiefly due to the *Zostera*. This theory has since been further dealt with in the Report of the Danish Biological Station, Nr. XX, 1911, in a paper by Joh. Petersen and Boysen Jensen, where the writers endeavoured to show that in all probability, the plants of the *Zostera* belt, and not the plankton organisms, should be regarded as the main sources of the organic matter of the sea bottom in our waters, and more especially in the Limfjord.

The proofs submitted, in the paper referred to, in support of this view, were as follows: The quantity of carbon in a series of bottom samples from Danish waters was determined, with the result that a proportional relation was found to exist between the abundance of *Zostera* vegetation in each locality and the quantity of organic deposit: not, however, between this latter and the density of the plankton. The obvious conclusion was that the *Zostera* must be the main source of the organic matter in the sea bottom.

This proof could, however, only be regarded as of a purely preliminary nature. In view of the importance of the question I have now, at the instigation of the Director of the Biological Station, Dr. C. G. Joh. Petersen, proceeded to a more detailed investigation of the problem, with the object of obtaining more definite proof of the theory concerned.

That the *Zostera* must play a not unimportant part in the production of matter in the sea is at once evident from the fact that in all Danish waters fragments of *Zostera* are found deposited on the bottom in more or less considerable quantities. The greater part of the organic matter is, however, deposited on the sea bottom in very fine particles, as detritus. If it were possible to determine, by microscopic examination of the bottom, whether the organic particles were fragments of *Zostera* or plankton organisms, this would be the simplest method of solving the problem. Such examination, however, does not furnish any fully satis-

factory result. It can be demonstrated with certainty that *Zostera* fragments are to be found, and often in very considerable quantities, whereas the quantities of diatom shells are a rule only very small. The great majority of the organic particles, however, are so fine that they might be derived from either *Zostera* or plankton organisms.

The only method of solving the question would thus appear to be by a chemical investigation of the bottom. In commencing this investigation, I have taken for granted that if characteristic differences could be shown to exist between the *Zostera* and the plankton organisms with regard to chemical composition, it should then be possible, by examining the organic matter of the sea bottom, to determine whether its origin should be attributed to the one or the other of these two sources. The aim of such examination would be to determine the relation between the quantity of the organic matter and of certain characteristic elements, in the sea bottom on the one hand, and in the *Zostera* and plankton organisms on the other.

It should here be noted that the *Zostera* differs very distinctly from the plankton organisms with regard to the nature of the cell walls. The cell walls of the *Zostera,* as already mentioned in Report XX, contain a considerable quantity of pentosans, whereas those of the diatoms are composed mainly of silica, those of the peridineans being fairly pure cellulose. The cell walls of the peridineans give a reaction with chlor-zinc-iodine. It would therefore seem that the proportion between the total quantity of organic matter and the quantity of pentosan must be far less in the case of the *Zostera* than in the case of the plankton organisms.

It is this relation which I have determined, partly by a series of *Zostera* and plankton samples, and partly by a series of bottom samples from Danish waters, with a view to ascertaining, by this means, whether the organic substances of the sea bottom are, in point of chemical composition, more nearly related to the Zostera or to the plankton organisms.

2. **Methods of chemical investigation**[1]). In order to estimate the quantity of organic matter in a given mass of material, I have determined the amount of carbon contained in the latter, these two values being on the whole proportional. Of the organic matter present in the plants, about 50 % is carbon. The carbon analyses have been carried out according to the method prescribed by Kjeldahl, which I have also previously employed in carbon analyses of the sea floor (cf. Report XX, p. 15, where the method is also further described). The values obtained by this means are often somewhat too low. In investigations of this nature, however, the absolute values are less important than the relative. Even where the separate analyses are subject to a constant error of about 5 %, this will be of no significance in comparing the two groups of analyses.

As a means of checking the work, however, I have also made a series of determinations of organic matter by burning this away and measuring the quantity of resultant ash. The material in question was first carefully dried at 100°, then charred in a flat crucible at as low a temperature as possible, the coal being then burned away at a slightly higher temperature. The quantity of organic

[1]) The chemical investigations have been carried out at the Plant-Physiological laboratory of the University. My best thanks are due to Professor W. Johannsen for his kindness in placing the laboratory and apparatus at my disposal for the work.

matter is then found as the difference between the quantity of dry matter employed and the amount of ash. This method gives very constant results; it can, however, only be employed for analyses of *Zostera* and plankton organisms: not for analyses of the sea bottom, as in the bottom samples there will almost invariably be a certain amount of clay, containing some water, which last is only given off by burning, together with the carbon. The values obtained by the analyses would therefore, in this case, be too high.

The pentosan analyses were carried out according to the usual method, by distillation with hydrochloric acid having a specific gravity of 1,06 (about 12%). The sample is distilled with 100 ccm hydrochloric acid of the strength referred to; for every 30 ccm of acid distilled, the same quantity is added, in order to maintain a constant amount of liquid in the retort. The process is continued until 400 ccm have been distilled. In the course of distillation with hydrochloric acid, the pentosan throws off furfurol, which is carried over with the vapour from the water and the hydrochloric acid. When the distillation is finished, the distilled liquid is filtered, and to it is added a quantity of floroglucin, dissolved in hydrochloric acid, amounting to at least twice the amount of the furfurol in the distillate. After some time, an almost black sediment of furfurol-floroglucin is gradually deposited: after a lapse of 24 hours this is filtered off in a filter which has been dried and weighed; the filter is then dried at 100° and again weighed. From the weight of this precipitate it is possible to calculate the quantity of pentosan in the amount of matter employed; this is done by means of a table compiled by Krøber, which may be found in Handb. der biochem. Arbeitsmethoden, published by Abderhalden, Vol. II, p. 154. When the weight of the deposit is less than 30 mgr then the quantity of pentosans may be calculated by the formula $(a + 0{,}0052) \cdot 0{,}8949$, where a is the weight of the precipitate.

Both the quantity of carbon and the quantity of pentosan are calculated as percentages of the dry matter. Dividing the percentage of carbon by that of the pentosan, we obtain the value of the quotient $\frac{C}{\text{Pentosan}}$; the value of the quotient is lowest in the case of organisms containing the greatest quantity of pentosan.

3. **Determination of the value for $\frac{C}{\text{Pentosan}}$ in Zostera.** This value was determined in the case of 5 different samples of *Zostera*. The result of the analyses is shown in the accompanying comparative table (Table 1)[1]: the figures from which the values here given have been calculated will be found in separate tables (Tables 12 and 13) at the end of this paper.

Table I. Zostera samples.

	C	Organic matter	Pentosan	$\frac{C}{\text{Pentosan}}$	$\frac{\text{Organic matter}}{\text{Pentosan}}$
Green *Zostera*, Nyborg Fjord, $^{11}/_{2}$ 13 .	33,9 %	73,8 %	8,4 %	4,04	8,8
Brown *Zostera*, Nyborg Fjord, $^{11}/_{2}$ 13.	30,7 %	74,0 %	8,4 %	3,68	8,8
Dead weed, Nyborg Fjord, $^{11}/_{2}$ 13	33,0 %	76,5 %	7,6 %	4,35	10,1
Brown *Zostera*, Svendborgsund 1912 .	29,2 %		7,6 %	3,84	
Fine particles of *Zostera*, S. of Grenaa Harbour, $^{28}/_{4}$ 13.....	29,6 %	65,2 %	6,3 %	4,70	10,4

[1]) The figures in this and the following tables have been worked out with a computer.

The three first analyses were made with *Zostera* samples all taken from the same locality, viz Nyborg Fjord, the samples being, however, at different stages of decomposition, the purpose of the analyses being to ascertain how far the value of the quotient $\frac{C}{\text{Pentosan}}$ underwent any change during the process of decomposition. The figures show that the changes are in any case not very great. True, the finest *Zostera* sample, the dead weed, exhibits the smallest quantity of pentosan, and consequently the highest value for the quotient in question; the difference is, however, so small as to lie in all probability within the limits of possible error.

We have also an analyses of brown *Zostera* from Svendborgsund; this gives approximately the same result as that of the corresponding sample from Nyborg Fjord. Similarly, an analysis of fine *Zostera* from the foreshore south of Grenaa Harbour closely resembles that of the dead weed from Nyborg Fjord.

Taking all the analyses together, we find that the value of the quotient $\frac{C}{\text{Pentosan}}$ varies between 3,7 and 4,7. It will further be noticed, that this quotient is very nearly proportional to the quotient $\frac{\text{Organic matter}}{\text{Pentosan}}$, which was also to be expected.

4. **Determination of the value for $\frac{C}{\text{Pentosan}}$ in plankton organisms.** As shown in Table I, the quotient values for the *Zostera* analyses are fairly constant. On the other hand, it is for various reasons quite impossible to obtain constant values in analyses of plankton. In the first place, the plankton samples are extremely heterogeneous, each separate sample being probably always composed of a number of different species. In any case, it is of course necessary to distinguish between the three main groups of plankton organisms; the diatoms, peridineans, and copepods, and endeavour to arrive at the value of the quotient for each. In addition to this, the treatment to which the plankton samples have been subjected prior to analysis is also of very great importance. This will be further explained when dealing with the separate analyses (cf. Table 2 and Tables 14 and 15).

Table 2. Plankton samples.

	C	Organic matter	Pentosan	$\frac{C}{\text{Pentosan}}$	$\frac{\text{Organic matter}}{\text{Pentosan}}$
Chætoceras pl., $^{31}/_{5}$ 11, The Sound ...	10,25 %		0,63 %	16,3	
Peridinean pl., $^{8}/_{10}$ 13, Svendborgsund,	22,0 %	47,0 %	1,22 %	18,0	38,5
Copepod- and peridinean pl., $^{16}/_{6}$ 13, Fænø Sund	14,1 %		1,52 %	9,3	
Chaetoceras pl., Oyster Basin, Nykøbing Mors, $^{20}/_{7}$ 13.....	11,0 %		1,02 %	10,8	
Chaetoceras pl., Oyster Basin, Nykøbing Mors, $^{22}/_{7}$—$^{14}/_{8}$ 13.....	11,7 %	27,2 %	1,24 %	9,4	21,9

The first analysis was made with chaetoceras plankton, taken in the Sound on the $^{31}/_{5}$ 1911. The sea water was at once filtered off as thoroughly as possible,

first by means of the plankton net, and afterwards with a filter paper. The plankton remaining on the filter was then dried, first at 60° and later at 100°. The dry matter thus obtained was then subjected to analysis. By this process, all loss of organic matter in the plankton organisms is avoided. The quotient value here obtained was 16,3.

A similar method was employed in the case of a sample of peridinean plankton from Svendborgsund. The plankton was preserved in alcohol; the whole sample however, was dried by evaporation, here again ensuring against any loss of organic matter. The quotient was 18,0.

The three last plankton samples, however, were treated in a different manner. The samples were preserved in alcohol, highly diluted. Before commencing the analysis, the alcohol was filtered off, and only the mass of plankton remaining on the filter was dried and analysed. By this process, naturally, all the organic matter soluble in dilute alcohol is lost. The quotient values were in this case very low, varying between 9,3 and 10,3. This is probably due to the fact that the matter dissolved is chiefly the contents of the cells, the wall substance remaining. The material is thus rendered relatively richer in pentosan, the quotient values being diminished.

The analyses show that both diatoms and peridineans contain pentosans. If diatom shells be treated with fluoric acid, which dissolves the silica skeleton, a very thin membrane is left, which gives no reaction with chlor-zinc-iodine. It is thus natural to suppose that this membrane may be formed of pentosan. The cell walls of the peridineans give, as already mentioned, a reaction with chlor-zinc-iodine. Probably however, this again is not »pure cellulose« but a more complicated compound, also containing some pentosan.

5. **Determination of the quotient $\frac{C}{\text{Pentosan}}$ in bottom samples.** In analysis of bottom samples again, constant quotient values are unobtainable, the reason here, however, being very different from that in the case of the plankton analyses.

Table 3. Bottom samples.

	C	Pentosan	$\frac{C}{\text{Pentosan}}$
Nyborg Fjord, upper layer, 16,5 m, $^{21}/_{10}$ 12	2,3 %	0,42 %	5,5
Nyborg Fjord, upper layer, washed, 21 m, $^{24}/_{9}$ 13	5,4 %	0,83 %	6,5
Detritus, Thisted Bredning, 1910	2,8 %	0,49 %	5,7
Livø Bredning, off Ørodde, upper layer, 1911	3,7 %	0,53 %	7,0
Livø Bredning, upper layer of bottom from oyster beds, $^{9}/_{9}$ 13	2,1 %	0,28 %	7,5
Kattegat, N. of Funen, upper layer, $^{20}/_{8}$ 12	5,5 %	1,06 %	5,1
Kattegat, E. of St. Middelgrund	2,5 %	0,29 %	8,6

The bottom analyses (cf. Tables 3 and Tables 16 and 17) fall into three groups. The first group comprises two samples from Nyborg Fjord, where *Zostera* growths abound. At a depth of 16 m.. a quotient of 5.5 was obtained, and at 21 m., the quotient was 6.5. To this must be added a sample of detritus from Thisted Bredning, taken in a detritus collector (for description of this, vide Report XX, p. 27). The quotient value for this sample was 5.7. The second group consists of two samples from Livø Bredning, which must be described as a fairly open water, with growths of *Zostera* along its edges only. The quotient values were 7.0 and 7.5. Finally, the third group is made up of two samples from the Kattegat. Of these one was taken comparatively close in to land, and has a very low quotient value, viz 5.1. The other sample was taken from the blue clay in the deepest part of the Kattegat. This sample gives the highest quotient value found, viz, 8.6.

From the analyses it would seem that a rise of the quotient value may be discerned from the more sheltered to the more open waters. The quotient values for these analyses vary between 5.5 and 8.6.

6. **Origin of the organic matter of the sea bottom.** The aim of the analyses above quoted was, it will be remenbered, to ascertain how far the organic matter of the sea bottom originated from the *Zostera* or from the plankton organisms. The analyses were intended to show whether the organic substances of the sea bottom more resembled the *Zostera* or the plankton organisms in regard to the amount of pentosan contained.

The quotient values varied, in the *Zostera* analyses, between 3.7 and 4.7. In comparing the quotient values for the *Zostera* with those for the sea bottom, the comparison should of course be based upon the analyses of the finest of the *Zostera* samples, these representing the stage most nearly approaching the organic matter of the sea bottom itself. We have two such analyses, the quotient values of which are 4.35 and 4.70, giving an average of 4.5. This value we may then take as typical for the *Zostera* in the form in which it enters into the composition of the sea bottom.

In the case of the plankton organisms, it is far more difficult to set up any such typical value. It must be presumed that the plankton organisms, before reaching the bottom, have not only given off such of their component substances as are soluble in sea water, but have also been more or less destroyed by bacteria. It is obviously impossible to obtain for purposes of analyses any samples of plankton thus extracted and transformed exactly in accordance with the processes which take place in the sea itself. It would beyond doubt be a mistake to employ the high quotient values, 16.3 and 18.0, obtained for plankton samples containing their full quantum of organic matter, as a basis for comparison. I am, however, inclined to believe that the analyses of the plankton samples extracted in dilute alcohol would furnish quotient values suitable for the purpose, and probably not too low. Even if the sea water does extract certain proteid substances to a higher degree than dilute alcohol, the alcohol, on the other hand, dissolves many substances which are insoluble in water. And as regards the bacterial transformation which the plankton organisms may undergo, we must suppose that they would in at least as high a degree affect the pentosan substances as the other organic

matter which the organisms contain, so that such transformation would scarcely occasion any reduction in the quotient values. This will be further referred to later on. Of plankton samples extracted with alcohol we have three quotient values, 9.3, 9.4 and 10.3, giving an average of about 10. This value may thus presumably be taken as typical for the plankton organisms in the form in which they enter into the composition of the sea bottom.

Between the value for the *Zostera*, 4.5 and that for the plankton, 10, lie the quotient values for all the bottom samples examined. If we could take it for granted that the organic substances of the sea bottom did not suffer any change, we should then be able to calculate, on the basis of the analyses made, the quantity of *Zostera* or plankton contained in the organic matter of the sea bottom at each of the localities investigated. We cannot here employ the quotient values; the quantity of pentosan must be calculated as a percentage of the quantity of C. We then obtain the following results:

Table 4.

	Percentage of *Zostera*	Percentage of plankton-organisms.
Average of the 3 first analyses (Nyborg Fjord og Thisted Br.)	57	43
Livø Bredning (Average)	31	69
Kattegat, N. of Funen	78	22
Kattegat, E. of St. Middelgrund	15	85

The figures here given are, as already mentioned, subject to the presumption that the organic substances of the sea bottom do not suffer any change. This is, however, not correct. There is no doubt that a very considerable transformation takes place in the organic matter of the sea bottom, and there is reason to believe that this metabolism occasions a reduction in the proportion of pentosan to the total quantity of organic matter. This metabolism is effected partly through the agency of bacteria and partly by the bottom fauna.

It has been demonstrated (Rossi e Carbone 1908) that various bacteria are capable of fermenting pectoses. It would therefore be natural to suppose that some such decomposition of the pentosan compounds is effected through the agency of bacteria on the sea bottom. Possibly also, this process of decomposition may further embrace other organic substances there found. As will be seen, however, in the following chapter, the quantity of nitrogen in the sea bottom is relatively very great, which rather seems to indicate that it is the non-nitrogenous components, such as for for instance pentosan, which are decomposed by bacteria.

It has moreover been observed, that at several places in the uppermost layer of the sea bottom, spindle-shaped excrements of bottom fauna are to be found. A portion of the organic matter of the sea bottom must therefore have passed through an alimentary canal; as will subsequently be shown, bivalves are in all probability

capable of digesting pentosan, and it is thus natural to suppose that the process of digestion occasions a diminution of the quantity of pentosan in proportion to the total quantity of organic matter. In support of this theory, a single analysis may be cited. In August 1913, Cand. Grøntved collected a quantity of oyster excrements at Nykøbing, Mors. The oysters were taken at different places in the Livø Bredning, and were left standing all night in Petri dishes set in an aquarium. On the following morning, the excrements, which are easily recognisable by their spindle-shaped appearance, were drawn up with a pipette. In this way, excrements of 94 oysters in all were collected. The excrements consisted, as the microscopical examination showed, of almost pure detritus; the weight dried was. 2.4 gr. An analysis gave the following results:

Analysis for carbon.

0.6785 gr. showed 143.2 mgr. $CO_2 = 39$ mgr. $C = 5.8\ \%$ C.

Analysis for Pentosan.

1.4617 gr. showed 0.2 mgr. furoglucide (+ 5 mgr. dissolved in the precipitating liquid) = 4.84 mgr. pentosan = 0.33 %. The quotient $\frac{C}{\text{pentosan}}$ is 17.6.

In addition to this, the uppermost layer of the bottom was sampled by means of glass tubes (vide Report XX, p. 13) at the places where the oysters were taken. These bottom samples were mixed together, and on analysis were found to contain 2.07 % C. and 0 278 % pentosan, giving a quotient of 7.48.

Even though the first quotient, 17 6, may be somewhat uncertain owing to the small amount of furoglucide found on analysis, we may, I think, still fairly conclude that the quotient is higher in the excrements than in the sea bottom, and that a diminution in the quantity of pentosan must thus have taken place during the process of digestion.

From the foregoing, it is reasonable to suppose that the bottom fauna and bacteria effect a decrease in the proportion of pentosan compounds to the total quantity of organic matter; if this be the case, however, the values as stated in Table 4 for percentage of *Zostera* will then be too low. As to the extent to which they should be increased, we have naturally no means of forming a definite opinion.

From the figures given, however, I believe myself to be justified in concluding, that:

In the more sheltered waters, the fjords, and most of the »Bredninger« in the Limfjord, the organic matter of the sea bottom is to a pre-eminent degree formed by the *Zostera*.

In the more open waters, as for instance in the Livø Bredning, at least half of the organic matter of the sea bottom is probably formed by *Zostera*.

On the other hand, it is possible that the organic matter of the sea bottom in the deepest parts of the Kattegat is formed chiefly by plankton organisms; this is, however, by no means proved.

7. Calculation of the production of phytoplankton and Zostera per 1 m². In the foregoing, an attempt has been made to solve the problem; whether the organic matter of the sea bottom has its origin in the *Zostera* or in the plankton orga-

nisms, by means of chemical analysis of bottom samples. There is, however, another way, the idea of which was furnished by Dr. C. G. Joh. Petersen, who requested me to try it, viz: to endeavour to ascertain the amount of *Zostera* and phytoplankton per unit of area annually produced in a given water.

It is obvious, that the results obtained by any such calculation can only be regarded as of a purely preliminary character. The amount of material at present available is far from sufficient to enable us to determine with even approximate accuracy the actual extent of such production. The object of the calculations here given is merely to show how far we have as yet been able to pursue the study of this question. It should be added that this is not the first time such investigations have been made. Hensen has, in an investigation of the same preliminary nature (1887, p. 96) calculated that the annual production of organic dry matter per 1 m^2 amounts to 15—18 gr., exclusive of the quantity of phytoplankton consumed by the plankton fauna. The total production of phytoplankton is estimated by Hensen at 150 gr. per 1 m^2 per annum.

The following calculations are based upon: K. Brandt: Beiträge zur Kenntnis der chemischen Zusammensetzung des Planktons (Wiss. Meeresunters. N. F. III. Bd. Abth. Kiel, p. 43, 1900) and C. G. Joh. Petersen: Om Bændeltangens (*Zostera marina*) Aarsproduktion i de danske Farvande (Mindeskrift for Japetus Steenstrup, 1913).

Calculation of the production of phytoplankton per unit of area. The work by Brandt, mentioned above, contains detailed chemical investigations of the plankton material in 11 different quantitative plankton hauls taken at the »Heulboje« outside Kielerfjord, at different seasons of the year at 20 m. depth. A plankton net with an opening of 0.1 m^2 was used, this being lowered to the bottom and then drawn vertically up. According to Hensen's investigations, however, the quantity of water filtered by such plankton hauls is only 1.66 cbm. In order to ascertain the quantity of plankton per 1 m^2 of surface, the figures obtained must consequently be multiplied by 12[1]). The different plankton samples are analysed, partly by the microscope and partly by chemical treatment. For each sample, the number of diatoms, peridineans, and copepods contained is stated, in addition to which, it is possible to calculate, from various tables, the quantity of organic dry matter in each sample.

We begin by ascertaining the quantity of phytoplankton per 1 m^2 for the different months of the year. As we know, from the tables given by Brandt, the number of plankton organisms for most months of the year, such a calculation will be easily made, provided the quantity of organic dry matter contained in a given number of diatoms and peridineans can first be found. From the plankton samples V, VIII, IX and XI, which are predominantly composed of copepods, we can calculate that 182,000 copepods contain 0.5862 gr. organic dry matter; 100,000 copepods will therefore represent 0.3221 gr. of organic matter. The plankton samples Nos. II and III consist of 96 million peridineans and 158,000 copepods, and contain 2.0496 gr. organic dry matter. From this we can, by means of

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[1]) According to Hensen's later investigations, however, this factor for multiplication is possibly somewhat greater.

Table 5.

No. of Plankton sample.	Diatoms Quantity (in gr.) of organic dry matter per $^1/_{12}$ m^2 (calculated)	Peridineans Quantity (in gr.) of organic dry matter per $^1/_{12}$ m^2 (calculated)	Copepods Quantity (in gr.) of organic dry matter per $^1/_{12}$ m^2 (calculated)	Total of Plankton Quantity (in gr) of organic dry matter per $^1/_{12}$ m^2 (calculated)	Total of Plankton Quantity (in gr-) of organic dry matter per $^1/_{12}$ m^2 (found)
I	0,0001	0,2407	0,1804	0,4212	0,5342
II	0,0006	0,7383	0,2222	0,9611	1,0372
III	0,0005	0,8025	0,2867	1,0897	1,0124
IV	0,0001	0,2728	0,1417	0,4146	0,5666
V	0,0006	0,0803	0,1836	0,2645	0,1722
VI	0,4096	0,0080	0,0483	0,4659	0,4096
VII	0,0435	0,0048	0,0870	0,1353	0,2211
VIII	0,0001	0,0016	0,1063	0,1080	0,1089
IX		0,0481	0,2480	0,2961	0,2552
X	0,0352	0,1765	0,3575	0,5692	0,5125
XI	0,0001		0,0483	0,0484	0,0499

Table 6.

	I. Diatoms Quantity (in gr.) of organic dry matter per $^1/_{12}$ m^2	II. Peridineans Quantity (in gr.) of organic dry matter per $^1/_{12}$ m^2	III. Phytoplankton Quantity (in gr.) of organic dry matter per $^1/_{12}$ m^2	IV. Phytoplankton Quantity (in gr.) of organic dry matter per 1 m^2	V. Factor for reproduction $^0/_0$ per diem	VI. Production of phytoplankton in organic dry matter per 1 m^2
I. January ..				(1,42)	(1,2)	0,51
II. February .	0,0006 0,0001	0,0803 —	0,0809 0,0001	0,49	(1,2)	0,18
III. March....	0,4096	0,0080	0,4176	5,01	(20,0)	30,06
IV. April	0,0435	0,0048	0,0483	0,58	(17,0)	2,96
V. May	0,0001	0,0016	0,0017	0,02	(14,0)	0,08
VI. June.....				(0,21)	(11,0)	0,69
VII. July				(0,40)	9,3	1,12
VIII. August ..		0,0481	0,0481	0,58	21,8	3,79
IX. September	0,0001 0,0352	0,2407 0,1765	0,2408 0,2117	2,72	17,4	14,20
X. October ..	0,0006 0,0005	0,7383 0,8025	0,7389 0,8030	9,25	5,7	15,82
XI. November	0,0001	0,2728	0,2729	3,27	1,2	1,18
XII. December.				(2,35)	(1,2)	0,84
					Summa...	71,43

the weight found for copepods, calculate that 100 million peridineans contain 1,6049 gr. of organic dry matter. The amount of organic matter in the diatoms can be calculated from sample No. VI, which consists almost exclusively of diatoms. From this we find, that 100 million diatoms contain 0,01291 gr. of organic dry matter[1]). The accuracy of these figures can be tested by calculating the amount of dry matter contained in each of the plankton samples and comparing with the figures directly obtained. This has been done in the accompanying Table 5; it will be noticed that the figures as calculated correspond more or less to those here found by direct determination. I doubt if better figures could be obtained.

By means of the figures found, we can calculate the quantity of phytoplankton for nine months of the year; this has been done in Table 6, columns I, II and III, all of which show the figures directly found and which must therefore, to obtain the values for 1 m^2, be multiplied by 12. This has been done in column IV, where also interpolated values have been inserted for the months for which no investigations have been made.

We can now proceed to determine the quantity of organic dry matter produced by the phytoplankton in each separate month. For this purpose, the reproduction factor is employed, giving the daily increase in % of the mass of plankton. Investigations as to this factor have been repeatedly made by Karsten (1898, p. 12), Gough (1905, p. 340), Gran (1909, p. 1) and Apstein (1911, p. 135). I have here followed Gran's calculations, which, by the way, agree more or less closely with those of Apstein. Gran's investigations were made with three different species of *Ceratium,* and extend over a period from $^6/_7$ to $^{17}/_{11}$. I have calculated a mean value for each separate month; the resulting figures will be found in Table 6, column V. Unfortunately, this method only gives the reproduction factor for 5 months. For the month of March, when a great maximum of diatoms takes place, I have set the factor at 20, which figure, according to Karsten's investigation, is probably not far out. For the months from April to June I have calculated values by interpolation between 20 and 8,3. In December, January and February, the factor is without doubt exceedingly low: I have taken it as 1,2, which corresponds to the value for November. Most of these figures are of course mere estimates; on the whole, however, I do not think they will be found too low (save perhaps that for October, which should possibly be somewhat higher).

We have thus obtained what are in all probability fairly accurate figures for the quantity of phytoplanktion per month, with considerably less accurate figures for the rate of reproduction. We have still to deal with the final and most difficult stage; the calculation of the monthly production of phytoplankton. On consideration of the figures for the quantity of plankton it is evident that progressive reproduction only takes place to a very slight extent. If the reproduction were progressive, then the quantity of plankton say from August to September would, with a reproduction factor of 19,6, rise from 0,58 to 125 gr (equation: $x = 0{,}58 \cdot 1{,}196^{30}$); as a matter of fact, however, the increase is only from 0,58 to 2,72. Only in spring, when the great diatom maximum occurs, does progressive

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[1]) Brandt has made similar calculations and obtained figures more or less corresponding to these.

reproduction take place to any considerable degree. When therefore, as especially in the autumn, no progressive reproduction does take place, this must be due to the fact that great quantities of individuals are either devoured or otherwise so destroyed as to take no further part in the propagation. In calculating the extent of the production therefore, it is necessary to regard the quantity of plankton as a capital fund, which daily yields a certain percentage (= factor of reproduction) of its amount, this percentage being either deposited on the sea bottom or consumed by other plankton organisms. Presuming that the figures given for the quantity of plankton may be taken as averages for the months in question, we can then arrive at the monthly production by means of the equation:

$$\frac{\text{quantity of plankton} \times \text{factor of reproduction} \times 30}{100}.$$

By this means the figures shown in column VI of Table 6 have been obtained. On adding together the figures in this column, we find a total of 71,43 gr, which thus expresses the entire annual production of phytoplankton in gr. of organic dry matter per 1 m².

When a certain amount of capital is placed at interest, the actual sum in possession of the owner at the expiration of a given time will of course be equivalent to the original amount plus the interest accrueing. In the same way, it might be imagined that we should add to the amount of production as calculated above, the total quantity of phytoplankton for the course of the year (as obtained by adding the figures in column IV of Table 6 = abt. 30 gr.). This would, however, hardly be correct. On examining the figures more closely, we find that the quantity of plankton given off, and which is consequently either deposited or consumed (calculated by means of the equation: Quantity of plankton in a given month + production for the same month ÷ quantity of plankton in the following month) is sometimes less and sometimes greater than the calculated production, according as the quantity of plankton is increased or diminished. There is, however, nothing to prevent our calculating the production of plankton by this method as well; the results thus obtained will be very nearly the same as those arrived at by the former.

In referring, in the foregoing, to the »quantity of plankton« this is to be understood as embracing only the so-called »net plankton«. There is, however, as Lohmann has shown, a certain number, not altogether inconsiderable, of plankton organisms which pass through the plankton nets. In order to arrive at the annual production of all plankton, the figure already obtained, 71,43 gr. should be augmented by some further value; what this value may be, however, it is unfortunately in all probability quite impossible to say. If we increase the quantity found by about 50 % we obtain something like 100 gr. I have thus arrived at the conclusion (always bearing in mind that the calculation can only be regarded as purely preliminary) that the annual production of phytoplankton in Kielerfjord may be estimated at about 100 gr. of organic dry matter per 1 m².

Calculation of the production of *Zostera* per unit of area. We will now attempt to determine the production of *Zostera* in the same way as we have already done in the case of the plankton. Here, however, the work is considerably easier, the calculations having already been made in the paper by C. G. Joh. Petersen above referred to. According to these investigations, the amount

of *Zostera* per 1 m² produced at the most favourable season of the year is, in good localities, 6000 gr.; in moderately good localities 3500 gr. and in bad localities 1700 gr., weighed throughout in fresh condition. The annual production is at least twice the amount here found. The percentage of dry matter in *Zostera* being 16, we can thus, according to Petersen, place the annual production of dry matter as at 1920, 1120 and 344 gr. at good, moderate and bad localities respectively.

Unlike the plankton, the *Zostera* has its area of occurrence limited to a belt along the coasts. Deposits of *Zostera*, however, take place in all Danish waters, the leaves, when torn away, being carried far and wide, and thus distributed over the whole of the sea bottom. The question then arises: what is the quantity of *Zostera* produced per 1 m², reckoning the production as for the entire extent of a certain water taken as a whole; say the waters between the Skaw and the Baltic (the line Gedser—Darsserort).

We reckon the *Zostera* beds as producing on an average 1120 gr. of dry matter annually. *Zostera* contains about 25 % ash. Expressed in organic dry matter, we have thus an annual production of 840 gr. pr. 1 m². In the water in question, about $^1/_7$th of the area consists of *Zostera* beds. The annual production of *Zostera* per 1 m² of the water as a whole is thus 120 gr. organic dry matter.

Production of *Zostera* and of Plankton compared. We have now arrived at the result, that the production of plankton may be taken as 100 gr. and that of the *Zostera* as 120 gr. organic dry matter pr. 1 m² in the waters inside the Skaw. With regard to the question as to how much of the matter thus produced is deposited on the sea bottom, there is, however, no doubt that the plankton production in particular will have to be very considerably reduced. In the first place, there will doubtless be a quantity, by no means insignificant, of plankton organisms which are dissolved when life is extinct, while others again are destroyed by the action of bacteria. Even supposing that a portion of the *Zostera* production is similarly lost, there is no doubt that the plankton organisms, with their relatively far greater surface, are in a much higher degree liable to destruction than the *Zostera*. In addition to this, however, considerable numbers of the plankton organisms are doubtless devoured by the plankton fauna. The quantity of plankton fauna amounts to about 50 % of the total quantity of plankton, so that the mass of food consumed by them can hardly be so insignificant a factor. (Lohmann is of opinion that the phytoplankton is, in certain months of the year, insufficient to supply the plankton fauna with food). There is thus no doubt that only a limited portion of the plankton production is deposited on the sea bottom; how large a portion this may be, however, it is impossible to say.

Altogether, it seems to me that the result of these calculations agrees, in all essentials, with the result obtained by chemical analysis of the organic matter in the sea bottom, which may be expressed as follows: In the more sheltered waters, the organic matter of the sea bottom is derived almost exclusively from the *Zostera;* in more open waters, it is possible that the plankton organisms may play a not altogether unimportant part as a source of the organic matter of the bottom.

II. Transformation of Nitrogen during decomposition of the Zostera.

1. **Introduction.** In the last chapter, we endeavoured to show that the organic matter of the sea bottom owes its origin in a very essential degree to the *Zostera*, adducing in proof the fact that the amount of pentosan contained in the organic matter of the bottom corresponds, in several places, very closely to the amount of pentosan contained in the *Zostera*. It is obvious, that instead of determining the relation between the quantity of organic matter and that of the pentosan compounds, we might also have taken other relative values, as for instance that of carbon and nitrogen, the quotient $\frac{C}{N}$. The value of this quotient also might be supposed to be the same in the sea bottom as in the *Zostera*.

The value of this quotient has already (Report XX, pp. 16—18) been determined for a number of bottom samples; it varied betwen 8,1 and 12,6, with an average of 11,1. I therefore examined some samples of green *Zostera*, and found that the quotient $\frac{C}{N}$ had approximately the same value in these.

It is, however, not the green *Zostera*, but the dust-fine, decomposed particles of the same which must be examined in order to arrive at a comparison between the *Zostera* and the organic matter of the bottom. On analysis of such samples of *Zostera* it was found that the quotient $\frac{C}{N}$ was considerably greater than in the sea bottom, in addition to which, the quotient for the green *Zostera* was likewise found to vary considerably. The whole question therefore required to be thoroughly investigated.

2. **Zostera analyses from Nyborg Fjord.** In order to further elucidate this part of the problem, 10 different samples of *Zostera* were collected in Nyborg Fjord in January 1913, these being intended to represent the same number of transition stages from the living grass wrack to the dead weed. The samples were numbered from 1—10, and temporarily classified as follows:

1. Living *Zostera;* all leaves green.
2. Main portion living; some few brown tips.
3. Main portion dead, but with some few green leaves still remaining; the dead leaves grayish-yellow in colour.
4. Leaves yellow; still some, however, of a greenish tint.
5. Leaves dark brown, but still largely whole.
6. 7. 8. But slight difference between these samples: the leaves have commenced to break into smaller pieces, but are for the most part still largely whole. Colour a light brown.
9. Considerable admixture of small particles, but many leaves yet whole.
10. Dead weed, consisting mainly of small fragments.

The samples were dried at 60°; the amount of dry matter in each was then determined, a small portion of the sample being dried at 100°. All the results of analyses are reckoned in percentages of the absolute quantity of dry matter.

The analyses for organic matter, carbon, and nitrogen were carried out as described in the foregoing. The quantity of nitrogen contained in the samples was determined by the quotient $\frac{\text{organic matter}}{\text{nitrogen}}$ and $\frac{C}{N}$; these two quotients are, as might be expected, on the whole proportional.

The results of the analyses are shown in Table 7. The special figures (Tables 18 and 19) will be found in the Table at the and of this paper.

Table 7. Zostera samples, Nyborg Fjord, January 1913

	Percentage of organic matter in the dry matter.	Percentage of N in the dry matter.	$\frac{\text{Organic matter}}{\text{nitrogen}}$	Percentage of C in the dry matter.	Percentage of N in the dry matter.	$\frac{C}{N}$
1	73,8	2,97	24,8	33,9	2,97	11,4
2	75,2	2,05	36,8	34,6	2,05	16,9
3	75,8	1,10	68,9	33,8	1,10	30,7
5	74,0	0,88	84,0	30,7	0,88	34,9
7	72,8	1,16	62,7	31,8	1,16	27,5
9	56,8	0,99	57,2	28,5	0,99	28,7
10	76,5	1,39	55,0	33,0	1,39	23,7

It will be seen from the analyses, that the live *Zostera* is exceedingly rich in nitrogen, containing about 3 %, or approximately the same percentage as is found in highly nitrogenous seeds, such as peas. The quantity of nitrogen is greatly diminished when the plants die; it is at its lowest in sample No. 5, which has 0,88 %; in samples at a still more decomposed stage it rises again, reaching in the dead weed a value of 1,39 %. The quantity of organic matter or carbon being about the same in all samples (with the exception of No. 9), then the value of the quotient $\frac{\text{organic matter}}{\text{nitrogen}}$ and $\frac{C}{N}$, which is lowest in sample No. 1, where the amount of nitrogen is greatest, will first increase, and then again decrease; this is also seen to be the case from the figures for the quotients referred to, as given in Table 7.

The series of *Zostera* samples here referred to were collected in the month of January. In order to ascertain what conditions might be found to exist at other seasons of the year, a new series of 4 samples was taken at the end of September. These samples were classified on the spot as follows. No. 1, green *Zostera,* still rooted to the bottom; No. 2, yellow; No. 3, brown; and No. 4, black *Zostera* or dead weed. The analysis was made in exactly the same manner as above described, only the value of the quotient $\frac{\text{organic matter}}{\text{nitrogen}}$, however, being determined. The result of the analyses is given in Table 8 (cf. Tables 20 and 21).

Table 8. Zostera samples from Nyborg Fjord, $^{24}/_{9}$ 13.

	Percentage of organic matter in the dry matter	Percentage of N in the dry matter.	$\frac{\text{Organic matter}}{\text{Nitrogen}}$
1.	72,6	1,35	53,8
2.	69,0	1,23	56,1
3.	64,6	1,15	56,1
4.	54,5	1,33	41,0

On comparing Tables 7 and 8, we find the following: The quantity of nitrogen in sample No. 1, the green *Zostera*, is considerably less in the September series than in that from January. The difference is so great that it can scarcely be due to mere coincidence. It is possible that the amount of nitrogen in the *Zostera* varies to some extent in the course of the year, which might possibly have some connection with the variation which is perhaps found in the quantity of in organic nitrogenous compounds in the sea water. This will be further investigated later on. The samples Nos. 2, 3 and 4 from the September series agree, as regards the amount of nitrogenous substances, fairly well with the corresponding samples (Nos. 3, 7 and 10) from the January series. In the former, however, there is a far greater quantity of ash, and therefore less organic matter than in the latter. For this reason also, we find that the value of the quotient $\frac{\text{organic matter}}{\text{nitrogen}}$ is, on an average, less for the September series than for the January. A point of especial importance, however, is the fact that the most highly decomposed *Zostera* is, also in the September series, relatively richer in nitrogenous matter than the half decomposed.

3. **Zostera analyses from the Limfjord.** In order to further ascertain the conditions prevailing at a different locality, two series of 4 samples each were taken in the Limfjord in the months of July and September 1913. No. 1 is green *Zostera*, Nr. 2 yellow, No. 3 brown, and No. 4 black *Zostera* or dead weed. The result of the analyses is shown in Tables 9 and 10 (cf. Tables 22 and 25).

Table 9. Zostera, Limfjord, W. of Mors, $^{21-23}/_{7}$ 13.

	Percentage of the organic matter in the dry matter	Percentage of N in the dry matter	$\frac{\text{Organic matter}}{\text{Nitrogen}}$
1.	79,4	0,83	95,8
2.	59,5	0,62	96,0
3.	50,5	0,66	76,5
4.	55,3	0,95	58,4

Table 10. Zostera samples, Nykøbing M., Bay. $^{12}/_{9}$ 13.

	Percentage of organic matter in the dry matter	Percentage of N in the dry matter	$\frac{\text{Organic matter}}{\text{Nitrogen}}$
1.	71,6	1,46	49,2
2.	66,8	0,71	94,0
3.	74,8	0,96	77,8
4.	59,1	1,49	39,8

The tables show that the green *Zostera* is richer in nitrogen in the September series than in that for July, which agrees well enough with the result of the Nyborg samples. For the rest, the two samples from the Limfjord agree fairly well, and both again indicate that the black and most decomposed *Zostera* is relatively richer in nitrogen than the brown, half decomposed samples.

Furthermore, an analysis was made of a *Zostera* sample even finer than the dead weed. A sample was taken on the 28th April 1913, from the weed washed up on the foreshore south of Grenaa harbour, and the finest particles sifted out. A microscopic examination of the sample thus obtained showed that it consisted of small particles of *Zostera*, containing, however, a certain admixture of fragments of algae, limbs of crustaceans and other matter. The analysis showed that the dry matter contained 29.6 % of C., 65.2 % of organic substances and 2.2 % of N. The quotient $\frac{\text{organic matter}}{\text{nitrogen}}$ was 29.6 and the quotient $\frac{C}{N}$ 13.4. This sample was thus relatively very rich in nitrogen.

The results of the analysis quoted may be summarised as follows: The amount of nitrogen in the green, fast rooted *Zostera* exhibits a certain variation (according to season?) and is in some cases fairly considerable. In the brown *Zostera*, the quantity of nitrogen is relatively very small, increasing again, however, in the highly decomposed weed. The decomposition of the *Zostera* is at first (in two of the analyses) accompanied by a decrease in the relative quantity of nitrogen, this being, however, subsequently (in all analyses) replaced by an increase in the relative amount of nitrogen contained.

To this it might perhaps be objected that each series of analyses contains samples of *Zostera* which can hardly have grown at the same time. In a series of samples taken, say, in January, the green *Zostera* will have grown in December-January, whereas the brown and black weed taken at the same time will be of an earlier growth. In view of the possible variation in the amount of nitrogen contained by green *Zostera* in the course of the year, this might be regarded as having some influence on the result. This objection may, however, be met by taking the average of all analyses; the samples being taken at different seasons, any seasonal variation in the quantity of nitrogen contained by the green *Zostera* will thereby be eliminated.

Table 11. Percentage of Nitrogen in the organic matter.

	Zostera-samples, Nyborg. Jan. 1913 (1, 3, 7, 10)	*Zostera*-samples, Limfjord, $^{21-28}/_{7}$ 13	*Zostera*-samples, Limfjord, $^{12}/_{9}$ 13	*Zostera*-samples, Nyborg Fjord $^{24}/_{9}$ 13	Average
1.	4,02	1,04	2,04	1,86	2,24
2.	1,45	1,04	1,06	1,78	1,33
3.	1,60	1,30	1,28	1,78	1,49
4.	1,82	1,72	2,52	2,44	2,13
Dust-fine *Zostera*, S. of Grenaa harbour, $^{28}/_{4}$ 13					3,36

The clearest view is obtained by calculating the amount of nitrogenous matter as a percentage of the organic matter. This has been done in the accompanying Table 11, for all four series of analyses. In addition, an average has been calculated for each separate stage of the process of decomposition.

The average figures reveal the same conditions as indicated by the separate analyses; the amount of nitrogenous matter decreases in the first stages of decomposition, only to increase again later on.

A graphical illustration of this is furnished by the accompanying figure (Fig. 1.).

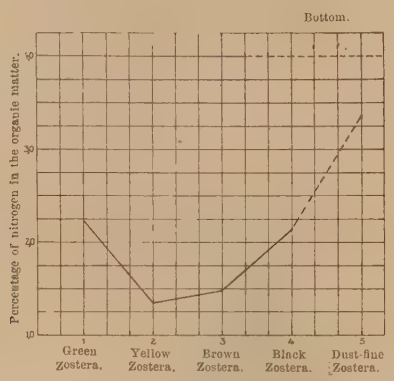

Fig. 1.

4. Transformation of nitrogen during decomposition of the Zostera. We may now return to our previous theory, viz: that the organic matter of the sea bottom, in any case at certain places, is predominantly derived from the *Zostera*. It might therefore be supposed that the proportion of nitrogenous to organic matter would be the same for both bottom and *Zostera*.

As mentioned at the beginning of this chapter, the quotient $\frac{C}{N}$ varies, in the bottom samples examined, betwen 8.1 and 12.6, with an average of 11.1. From this we may reckon that the quantity of nitrogen amounts to about 4 % of the total quantity of organic matter in the sea bottom. This value is marked by the horizontal dotted line in Fig. 1.

From this we see that the organic substances of the bottom contain a greater proportion of nitrogen than the *Zostera*; it now remains to endeavour to explain why.

That the amount of nitrogen in the *Zostera* may be increased during decomposition has already been seen from the analyses above referred to, which we will now proceed to examine more closely (cf. Fig. 1). Beginning with the green weed, we find that there is a diminution of the relative quantity of nitrogen in the first stage of decomposition; it must be added, however, that such diminution has only been found in two of the four series of analyses. This falling off is presumably due to the fact that a portion of the nitrogenous protoplasm is dissolved in the sea water as the *Zostera* cells die. The yellow and brown *Zostera* contain only about $^1/_3$ of the percentage of nitrogenous matter found in the bottom itself. With the further decomposition of the *Zostera*, however, there is, as is

shown by the curve, and likewise uniformly indicated in all 4 series of analyses, an increase in the proportion of nitrogen. In the black *Zostera* (the dead weed) the relative amount of nitrogen is about half that found in the sea bottom. In the still finer sample from Grenaa, the amount of nitrogen is again considerably greater, approaching very nearly to that of the bottom itself. From this we may assume that the *Zostera*, as it becomes more and more disintegrated, simultaneously becomes more and more nitrogenous, until the amount of nitrogen contained very nearly approaches that of the bottom.

An increase in the proportion of nitrogen may be brought about in two different ways; either, 1) by the destruction of non-nitrogenous substances in the sea bottom to a greater extent than is the case with nitrogenous matter, or, 2) by the fixation of inorganic or free nitrogen. We will consider these two possibilities separately.

It is beyond all doubt that the non-nitrogenous substances of the sea floor are to a very considerable extent destroyed by bacteria: we have already mentioned, as an instance of such destruction, the probable fermentation of pectoses. Reference has also been made, in Report XX, to the formation of methane at certain places in the sea bottom, probably due to fermentation of cellulose. And we have previously cited reasons which suggest that the non-nitrogenous substances are affected by the action of bacteria to a higher degree than is the case with nitrogenous matter. This is probably due to the fact that the nitrogenous substances are comparatively easily transformed into humic compounds, which are less easily destroyed.

It is also possible that the excremental action of the fauna contributes to render the bottom richer in nitrogen. The sea bottom is, as will subsequently be seen, doubtless extremely poor in digestible forms of nitrogen, whereas digestible pentosan is found in very considerable quantities. It is thus possible that this admixture of indigestible nitrogenous matter may serve to render the excrements richer in nitrogen than the food itself. In support of this theory I may adduce an analysis of oyster excrements from the Limfjord. These excrements, which consisted of almost pure detritus, contained 5.8 % C and 0.71 % N, the quotient $\frac{C}{N}$ being thus 8.2. Bottom samples taken at the same place as the oysters were found to contain 2.07 % C and 0.187 % N. The quotient $\frac{C}{N}$ is thus 11.1, the same as is usually found in bottom samples. The excrements therefore contain a higher percentage of nitrogen than the sea floor. Of course, the result of a single analysis must be considered with all due reserve; it does, however, point towards the possibility of a relative increase in the quantity of nitrogen occasioned by the digestive process.

The nitrogenous matter of the bottom can also be increased by the fixation of inorganic nitrogen through the action of bacteria. Nitrogen may either be taken from the ammonia or nitric acid compounds dissolved in the water, or from the free nitrogen, which is also present in solution. It is a well-known fact that many bacteria can, when provided with suitable non-nitrogenous nourishment, obtain the requisite nitrogen for consumption from ammonia or nitric acid com-

pounds, by which the nitrogen is carried over into organic compounds. That such bacteria should exist in the sea bottom is at any rate very probable. It is also probable that in any case at certain parts of the sea bottom, a fixation of free nitrogen takes place. Keutner (1905, p. 29) and later Keding (1906, p. 273) have shown that such bacteria (*Azotobacter* and *Clostridium*) are of common occurrence in the Kielerfjord, partly on the bottom and partly on marine algae and plankton organisms. Liebert (1912 p. 3); who has later investigated the same question, denies, it is true, that *Azotobacter* should be of common occurrence in sea water; he also, however, is of opinion that it is possible, by infecting with blackmud from the sea bottom, to produce a strong fermentation to butyric acid with fixation of nitrogen. Liebert is of opinion that fixation of nitrogen does not play nearly so important a part in the sea as on land; he considers however, that in places where a rich vegetation is found, a considerable fixation of nitrogen may take place.

Finally, it may be pointed out that the fauna itself, by dying and forming detritus, also serves to increase the amount of nitrogen in the sea floor.

III. Determination of the total quantity of detritus and plankton in sea water.

A long series of determinations have already been made as to the amount of plankton in sea water, or rather, as to the quantity of such organisms as can be taken in a plankton net having a certain width of mesh. It is, however, generally agreed that this so called net plankton represents but a portion of the matter actually in suspension in the water. There are to begin with, as Lohmann (1908, p. 29) has shown, numerous organisms which pass through the plankton nets, and the same also applies to many lifeless particles of organic or inorganic matter, which may be comprised under the name of detritus.

In order to ascertain the total amount of suspended matter in sea water, it is necessary either to centrifuge the water or pass it through a very close filter. The method employed in the following investigations in that of filtration by means of hardened filters, which, besides being close, present the additional advantage that the sediment may be quantitatively removed by washing off with a spray.

Owing to the slight amount of suspended matter contained in sea water, at least 10 litres of each sample taken must be filtered. The filtration was carried out in the following manner: The sample of sea water was taken in a 10 litre bottle, and was at once sterilised by the addition of sublimate. It was then filtered in portions of 2 L. at a time. A two litre flask is filled, and closed with a rubber cork, pierced to receive two glass tubes (Fig. 2), one long(a), with a fairly small bore, and the other shorter(b), consisting of two pieces of tube cemented together, the bore of the one piece being small, that of the other fairly large. The flask is placed over the funnel containing the filter, the glass tubes projecting downwards into

the latter. The water then flows out through the tube *a*, air being simultaneously drawn up by way of *b*. When the water in the filter has risen sufficiently to close the aperture of *b*, the flow ceases, recommencing, however, as soon as enough water has passed through the filter to permit of the passage of air once more by way of *b*. The effect of this double tube system is to maintain a very constant water-level in the filter, which is almost continually filled nearly to the brim, a point of great importance as regards the rapidity of filtration. A grooved funnel is used, and glass plates are placed over it to prevent, as far as possible, any dust from falling into the water. A rubber tube is attached to the funnel to drain off the water.

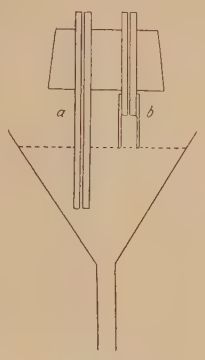

Fig. 2.

When filtering the first samples, the water flowed through at a fairly rapid rate, 5 L. of water passing without difficulty through a single filter. The samples from Nykøbing Mors, however, presented considerable difficulty, the filters very soon becoming impermeable, so that as many as 4 different filters were required for the filtration of 10 litres of water. When the filters could no longer be used, they were carefully rinsed with a spray, and the sediment placed in a glass-stoppered bottle and sterilised with sublimate. In order to determine quantitatively the amount of sediment in the different samples of sea water, the sediment was filtered off through a weighed filter, dried at 100° and weighed again, being first, however, examined under the microscope.

We have thus been able to ascertain the total quantity of detritus and plankton in the samples examined. Unfortunately, however, it is hardly possible to determine the respective quantities of the two separate components. To obtain detritus which is perfectly free from plankton is as impossible as to obtain plankton containing no detritus.

All the filtrations were carried out by cand. Grøntved.

The results of the determinations were as follows:

I. Water samples from Sallingsund, Limfjord, off Ørodde:

No. 1. 18 May 1912. Residue consisted predominantly of detritus; some few diatoms (*Chætoceras, Pleurosigma*). Weight of dry matter 15.6 mgr.

No. 2. 24 May 1912. Residue mainly detritus. Some few diatoms. Weight of dry matter 19.6 mgr.

No. 3. 4 June 1912. Mainly detritus. Some plankton (*Chætoceras, Rhizosolenia — copepods*). Weight of dry matter 10.7 mgr.

No. 4. 14 June 1912. Mainly detritus. Many organisms (*Pleurosigma, Prorocentrum* — copepods). Weight of dry matter 9.6 mgr.

No. 5. 21 June 1912. Principally detritus. Weight of dry matter 10.1 mgr.

No. 6. 28 June 1912. Almost pure detritus. Weight of dry matter 13.2 mgr.

No. 7. 4 July 1912. Almost pure detritus. Some few *Prorocentrum*. Weight of dry matter 12.3 mgr.

No. 8. 10 July 1912. Mainly detritus. Some organisms (*Rhizosolenia, Chætoceras Sceletonema*). Weight of dry matter 14.6 mgr.

No. 9. 22 July 1912. Predominantly detritus. Some few diatoms *(Rhizolsolenia, Chætoceras).* Weight of dry matter 48,0 mgr.

No. 10. 3 August 1912. Mainly organisms (principally *Sceletonema,* some few *Prorocentum*). Detritus. Weight of dry matter 23,5 mgr.

No. 11. 13 August 1912. Pure detritus. Organisms very rare. Weight of dry matter 73,8 mgr.

In addition, some filtrations were made of water from the oyster basins at Nykøbing Mors.

No. 1. 18 May 1912. Almost pure detritus (remains of *Zostera*!). Weight of dry matter 2,9 mgr.

No. 2. 24 May 1912. Almost pure detritus. Weight of dry matter 3,1 mgr.

No. 3. 3 June 1912. Detritus. Many organisms *(Sceletonema, Chaetoceras).* Weight of dry matter 16,9 mgr.

No. 4. 14 June 1912. Mainly detritus. Some few diatoms. Weight of dry matter 12,0 mgr.

No. 5. 25 June 1912. Detritus. Many organisms *(Sceletonema, Chaetoceras, Ceratium, Nauplier).* Weight of dry matter 10,4 mgr.

No. 6. 1 July 1912. Much detritus. Some organisms *(Sceletonema,* gastropod larvæ). Weight of dry matter 16,7 mgr.

No. 7. 9 July 1912. Much detritus. Some organisms *(Prorocentrum, Sceletonema, Ceratium).* Weight of dry matter 15,5 mgr.

No. 8. 6 August 1912. Much detritus. Some organisms *(Sceletonema).* Weight of dry matter 14,1 mgr.

The microscopic analysis shows that the water from the oyster basins is on the whole far richer in plankton organisms than that from the Limfjord. This can hardly be due to the difference of temperature; during the months from May—August the temperature both of the oyster basins and in the sea water was taken three times a day, with the result that the difference in this respect between the two localities was found to be generally extremely slight. The superiority of the basins in regard to quantity of plankton must therefore be due to other causes; possibly the water here contains more carbonic acid than the sea water, as a rich growth of algae was found at the bottom of the basins, and in consequence, a quantity of decomposing vegetable matter. Moreover, the water in the basins, though renewed by pumping, is devoid of all wave movement, a fact which may perhaps also be of some importance in this connection.

In the Limfjord samples, the filtered residue consisted mainly of detritus; only in one sample were plankton organisms found to predominate, as against which, several samples were composed of almost pure detritus. The analyses show that the quantity of residue is on the whole greatest in the latest samples, from July—August. I had imagined that it might perhaps be possible to prove some parallel relation between the force of the wind and the quantity of detritus. Even a merely macroscopic examination is sufficient to show that the water in most of the very shallow Danish fjords has, after a storm, a muddy appearance, evidently due to the suspended detritus. The strength of the wind was therefore noted

at the time when the filtration samples were taken. The wind was, on the whole, comparatively low during the period when the experiments were carried out, and on going through the material, no striking similarity was found to exist between the variation in the quantity of detritus and that in the strength of the wind. A fairly heavy storm is doubtless required to stir up the bottom.

It will be seen from the foregoing, that all the samples of sea water examined were found to contain rich quantities of detritus, and further, that the amount of detritus is on the whole far greater than that of the plankton organisms. It has not, however, been possible to make any quantitative determination of the detritus as compared with the amount of plankton found.

IV. The organic matter of the sea bottom as a source of nourishment for the benthos fauna.

As mentioned in Report XX from the Dan. Biol. St., it may doubtless be presumed that the organic matter of the sea bottom forms a source of nourishment for the majority of the fauna living in and upon the bottom. It may therefore be worth while to investigate the question as to how far suitable nourishment for such fauna can be shown to exist among the substances of which the sea bottom is composed.

1. **The chemical composition of the Zostera and plankton.** As has already been shown, the organic matter of the sea bottom must, in many places at least, be regarded as almost exclusively derived from the *Zostera*. It is therefore natural to commence with a closer examination of the chemical composition of this weed.

	Ash	Fat	Nitrogen	Pentosan
Zostera	abt. 25 %	not analysed	1,5 %	8–9 %
Hay	abt. 7 %	2,2 %	1,1 %	abt. 20 %

The table above shows the respective percentages of ash, fat, nitrogen and pentosan contained in the dry matter of *Zostera*, and of hay from various fodder grasses *(Lolium italicum, Avena elatior, Bromus arvensis, Dactylis glomerata, Festuca pratensis)*. The *Zostera* analyses are from my own investigations, those of the grasses being taken from investigations by Rørdam (1913, p. 365).

The figures show that the *Zostera* may fairly be compared with the fodder grasses. True, the percentage of ash is much higher; on the other hand, there is, it seems, on the whole also more nitrogen in the *Zostera* than in the hay. A percentage of nitrogen amounting to 1,5 % should, according to Rørdam's investi-

gations (in the grasses) correspond to abt. 7,5 % of proteids. The percentage of pentosan in the *Zostera* is only half that found in the hay. I have not analysed the *Zostera* for fat and cellulose.

I have moreover made some investigations as to the digestibility of the nitrogenous substances in the *Zostera.* 2 gr. of green *Zostera,* finely pulverised, (weight of dry matter 1,616 gr.) was allowed to stand for 5 days at a temperature of 30° with 80 ccm. of water + 160 ccm. pancreatin (»Rhenania«) + 2 ccm. toluol., 40 ccm. was then filtered off, and precipitated with barium chloride and hydrate of baryta in order to eliminate weak acids (Henriques, 1909, p. 2); the quantity of amides in the filtrate was determined by titration with formol (Sørensen, 1907, p. 1). It was then found that the quantity of nitrogen which could be titrated with formol amounted to 3,3 ccm. $\frac{n}{5}$ baryta. In a test sample, consisting of 80 ccm. water + 160 mgr. pancreatin + 2 ccm. toluol, which was left to stand for the same time and at the same temperature, the corresponding amount of nitrogen when similarly treated was found to be 1,7 ccm. $\frac{n}{5}$ baryta. From this we can reckon the quantity digested at 11,2 mgr. N = 0,69 %. The amount of nitrogen in the *Zostera* sample being 2,97 % it thus appears, that about 23 % of the quantity of nitrogen can be digested by pancreatin. In another experiment, about 26 % of the nitrogen was digested. As the *Zostera* contains about 7.5 % proteids, of which about $^1/_4$ is digestible by pancreatin, the amount of digestible proteids contained is thus found to be 1,8 % These figures should, however, in all probability mainly be taken as minimal.

The chemical composition of the plankton organisms I have not investigated, this question having been very thoroughly treated in the paper by Brandt (1900, p. 43) previously referred to. I quote here, from Brandt's investigations, the compositions of the autumn plankton of the western Baltic:

Proteids	Fat	Carbohydrates	Ash
20,2—21,8	2,1—3,2	60—68,9	8,5—15,7

In the course of decomposition of the *Zostera,* the quantity of nitrogenous matter is doubtless, as already noted, somewhat diminished. At the same time, the digestibility is also reduced; in the brown and black *Zostera,* the percentage of digestible nitrogen as compared with the total quantity of nitrogen is considerably less than in the green weed. In brown *Zostera,* only 0,089 % of digestible nitrogen was found (by digestion with pancreatin and titration with formol as above). This sample of *Zostera* contained in all 1,16 % of nitrogen; only 7,7 % of the total quantity of nitrogen is therefore digestible. In black *Zostera* (dead weed) 0,098 and 0,086 % of digestible nitrogen was found; the sample in question contained 1,39 % nitrogen, only 6,6 % of this being digestible.

2. **Digestible matter in the sea bottom.** We may now proceed to investigate the question as to how far the sea bottom can be shown to contain substances digestible by the fauna there found. The nitrogenous and non-nitrogenous compounds may be taken separately.

Digestible nitrogenous compounds in the sea bottom. Even in the black *Zostera*, the quantity of digestible nitrogen is so small as to be hardly discernible by means of formol titration. And for the sea bottom, where the percentage is still lower, this method cannot be used at all.

In order to demonstrate the existence of digestible matter in the sea bottom, I have adopted the following method: The bottom samples were taken by means of the glass tube referred to in Report XX (p. 13). The diameter of the tube was 2 cm.; its sectional area therefore being about 3 cm^2. Ten samples were taken from each locality, corresponding to a bottom area of 30 cm^2. These bottom samples were divided into two separate classes: The upper layer, consisting of the uppermost cm. (»The brown layer«), and the lower, comprising the 2 cm. immediately beneath. Both upper and lower layer samples were dried at 60° and finely pulverised. Each layer was then divided into two perfectly equal parts, *a* and *b*. The *a* portions of the upper and lower layers respectively were placed in 50 ccm. water + 50 mgr. pancreatin + 2 ccm. toluol, and left to stand for 8 days at 30°; the *b* portions were left to stand for the same time in 50 ccm. water + toluol (but no pancreatin!). In addition a test sample was set aside, consisting of 50 mgr. pancreatin + 50 ccm. water + 2 ccm. toluol. After the five samples had stood for 8 days, 25 ccm. of the liquid was filtered of from each, and precipitated with 5 drops of lead acetate and 5 ccm. tannic acid. After standing for 24 hours, 20 ccm. was filtered off, and analysed for nitrogen according to Kjeldahl's method.

On example may serve as illustration.

In Samsø Bælt, N. of Fynshoved (Lillegrund), 35 m. depth, a very rich *Abra* and *Macoma calcarea* station, ten glass tube samples were taken on the $^{22}/_{5}$ 1913, the total bottom samples representing an area of 30 cm^2. The samples were divided into upper and lower layers, as above described. The result of the analysis was as follows:

1. Surface layer.
   a. 3 gr. + 50 ccm. water + 50 mgr. pancreatin + 2 ccm. toluol.
      After standing for 8 days at 30° and being treated as above described, the quantity of nitrogen in the final filtrate corresponded to 1,80 ccm. hyposulphite solution.
   b. 3 gr. + 50 ccm. water + 2 ccm. toluol.
      Quantity of nitrogen corresponded to 0,00 ccm. hyposulphite solution.
2. Lower layer.
   a. 8 gr. + 50 ccm. water + 50 mgr. pancreatin + 2 ccm. toluol.
      Quantity of nitrogen corresponded to 1,00 ccm. hyposulphite solution.
   b. 8 gr. + 50 ccm. water + 2 ccm. toluol.
      Quantity of nitrogen corresponded to 0,10 ccm. hyposulphite solution.
3. Test.
   50 mgr. pancreatin + 50 ccm. water + 2 ccm. toluol.
   Quantity of nitrogen corresponded to 0,90 ccm. hyposulphite solution.

The quantity of nitrogen found in the final filtrate from the *a* portion of the surface layer may be derived from three different sources: 1) the action of the pancreatin upon the proteids of the bottom sample may have occasioned the

formation of nitrogenous compounds which are not precipitated by tannic acid (corresponding to the digestible nitrogen); 2) the bottom sample may contain nitrogenous compounds soluble in water even without the action of pancreatin (the amount of nitrogen in the *b* portion furnishes a hint as to the quantity of such compounds), and 3) the pancreatin may contain nitrogenous compounds which are not precipitated by tannic acid (the quantity of these compounds is determined by the amount of nitrogen found in the test sample). In order to arrive at the quantity of digestible nitrogen we must therefore subtract from the quantity of nitrogen found in *a* portion, the last two quantities; i. e., calculate the value of $1a \div 1b \div 3$. The amount of digestible nitrogen in the surface layer thus corresponds, in the example here given, to $1{,}8 \div 0{,}0 \div 0{,}9 = 0{,}4$ ccm. hyposulphite solution. From this we can reckon the contents as $1{,}74$ mgr. digestible N, corresponding to $10{,}9$ mgr. digestible proteids. In the lower layer, we have $1{,}0 \div 0{,}1 \div 0{,}9 = 0.0$.

The result of the analysis is therefore as follows:

The sea bottom contains, at the locality stated, in the upper layer 65 mgr. and in the lower 0 mgr. of digestible proteids per 100 cm.^{2} of surface.

In a similar manner, I have now made several analyses with the following result:

2. Bottom sample from Nyborg Fjord, outside Slipshavn, $^{25}/_{4}$ 1913.
   In the upper layer, 52 mgr. and in the lower, 0 mgr. digestible proteids per 100 cm^2 of surface.
3. Bottom sample from same locality as 2, taken $^{26}/_{8}$ 1913.
   In the upper layer, 44 mgr. and in the lower 0 mgr. digestible proteids per 100 cm.^{2} of surface.
4. Black mud from the bottom of Holbæk Fjord, $^{10}/_{6}$ 1913.
   In the upper layer, 68 mgr. and in the lower 0 mgr. digestible proteids per 100 cm^2 of surface.
5. Bottom sample from Venø Bugt, $^{22}/_{7}$ 1913.
   In the upper layer, 62 mgr. and in the lower 9 mgr. digestible proteids per 100 cm^2 of surface.

By titrating with formol, the quantity of amides formed by digestion of the proteids is directly determined; with the tannic acid precipitate, however, all that is ascertained is the fact that the action of the pancreatin on the proteids occasions the formation of substances which are not precipitated by tannic acid, no information being furnished by this method as to the actual nature of the substances in question. We have thus, especially when dealing, as in the present case, with very small quantities, no absolutely certain proof that the ascertained amount of nitrogen which is not precipitated by tannic acid really is derived from the decomposition of the proteids, although this is extremely likely to be the case.

The figures show that there is only a very small amount of proteids in the bottom which is digestible with pancreatin; the amount being, indeed, so small as to be very nearly within the limids of possible error. The different analyses of the upper layer, however, all give positive results, and I therefore think it justifiable to conclude that the uppermost layer of the bottom really does contain a certain amount of proteids digestible by pancreatin.

In the upper layer, from 44 to 68 mgr. digestible proteids per 100 cm^2

has been found; these figures must, however, as already indicated in the foregoing, only be regarded as approximate. The amount of digestible proteids per 1 m^2 should thus be 5 gr.

The main point in this connection is the question as to whether this quantity of proteids is sufficient to cover the proteid consumption of the detritus eaters of the sea bottom. As will be seen from the numerous quantitative valuations of the bottom fauna made by C. G. Joh. Petersen (1913, p. 3), the weight of living animal matter pr. 1 m^2, expressed in gr. of organic dry matter is very variable. It lies most frequently between 5 and 30 gr.; the greater part must doubtless be regarded as detritus eaters. The amount of the fauna is thus relatively very great in comparison with the quantity of digestible proteids found. Several points should, however, here be noticed: 1) The value obtained, 5 gr. per 1 m^2, indicates only the momentary amount; this is of course, frequently renewed, as new detritus is constantly being deposited. As to how often it is renewed, however, nothing is known. 2) The amount of digestible albumen has been determined by digestion with pancreatin. It is probable, however, that bivalves and other constant detritus eaters as may possess enzymes which react far more strongly upon the nitrogenous matter of the bottom than pancreatin preparations, which are taken from mammals, can do. There is therefore reason to suppose that the figures quoted above should be regarded as minimal values. 3) Finally, nothing is known as to how great the proteid consumption of the bottom fauna may be.

In the lower layer only very slight traces of digestible proteids have been found.

Digestible non-nitrogenous compounds in the sea bottom. In an earlier chapter, attention has been drawn to the fact that the sea bottom contains a fairly considerable amount of pentosan; from 0.3 to 1.0 %. This is also worthy of note in this connection, since there is reason to suppose that the bottom fauna are able to digest pentosan.

As to the digestibility of pentosan, we have already a series of works on the subject. Among earlier writers may be mentioned Salkowski (1901, p. 393) who found, that by feeding rabbits with pentosan compounds, a glycogene formation was obtained, a portion of the pentosan being, however, simultaneously discharged with the urine. Since then, Weiske (1895, p. 489) and Rudzinski (1904, p. 317) have made detailed investigations of the same subject. Both these writers found, that 46—83 % of the pentosan contained in the food disappeared in the course of its passage through the alimentary canal. The investigation was made with various herbivorous mammals, (sheep, rabbits etc.). These investigations, however, as Weiske also points out, furnish no proof that the pentosan really plays any part as a source of nourishment for the animals in question. It might easily be imagined that the pentosan became decomposed in the alimentary canal by the action of bacteria, or was passed out unchanged with the urine. These possibilities have been considered in a work by Slowtzoff (1901, p. 181), who fed his subjects with pure xylane. He found, that from 33.17 to 82.91 % of the xylane was absorbed in the alimentary canal, only 1.49—4.63 % being secreted in the urine. He also found that the xylane was very difficult to decompose, so it is hardly probable that it should be destroyed by bacteria in the intestines. We

may therefore probably conclude that the pentosan really is utilised by the animals in question.

The experiments hitherto referred to have been made with herbivorous mammals, and can naturally not be considered as similarly valid for bivalves. We have, however, the interesting investigations of Biedermann and Moritz (1898, p. 219) (cf. also Müller, 1901, p. 619) made, it is true, not with bivalves, but with gastropods, and demonstrating that these must also be considered as able to digest pentosan. The writers in question found, that the secretion from the liver of *Helix pomatia* contains diastase. This secretion was capable of fairly rapidly dissolving starch grains of wheat, rye, maize and rice; potato starch, however, remaining unaffected thereby. In addition, the cellulose membranes were also largely affected, from which we may conclude that the secretion also contained cytase. The secretion in question was also capable of dissolving the so called reserve cellulose in dates, and in *Phytelephas;* lignified membranes, however, and pure cellulose (cotton and paper) were not affected. As products of decomposition, besides hexoses, pentoses were also found, from which we may conclude that the secretion is also capable of digesting pentosan. Undissolved proteids, were, strangely enough, not affected.

We may then perhaps conclude that also bivalves are able to digest pentosan, and that the considerable amount of pentosan present in the sea bottom — besides other possible substances (hemicellulose generally) plays an important part as non-nitrogenous nourishment for a great portion of the bottom fauna.

V. Summary.

In a paper by C. G. Joh. Petersen and P. Boysen Jensen (Report XX from the Dan. biol. Stat.) the writers considered it proved, that the plant growths of the *Zostera* belt, and not the plankton organisms, should probably be regarded as the principal source of the organic matter of the sea bottom in many of our waters. This question has now been subjected to closer investigation.

By determination of the quantity of pentosan in proportion to the amount of organic matter it was found, that the *Zostera* was relatively far richer in pentosan compounds than the plankton organisms. The organic matter of the sea bottom was seen to occupy an intermediate position between the *Zostera* and the plankton with regard to the amount of pentosan contained. Closer consideration of this point led to the conclusion that the organic matter of the sea bottom in the more sheltered waters (fjords etc.) was almost exclusively derived from the *Zostera;* in more open waters, however, (e. g. the Kattegat) the plankton organisms are possibly of some importance as a source of origin for the organic matter of the sea floor.

At the instigation of D. Petersen I have moreover made certain calculations as to the quantity of plankton and *Zostera* produced per 1 m^2 in the waters

from the Skaw to the Baltic. By these calculations it was ascertained that the production of plankton amounts to about 100 gr., that of the *Zostera* to about 120 gr. per 1 m^2. It must be presumed that only a small portion of the plankton produced is deposited on the sea bottom. The deposits of plankton are probably more or less evenly distributed over the sea bottom, whereas the *Zostera* is mainly deposited in more sheltered waters. With regard to the question as to the origin of the organic matter in the sea bottom, the calculations made thus lead to very much the same result as was obtained by the chemical investigation.

The organic matter of the sea bottom contains more nitrogen than the *Zostera*. It must therefore be supposed that the *Zostera* becomes relatively richer in nitrogen during the process of decomposition. Closer investigation of four series of *Zostera* samples at different stages of decomposition also showed that the highly decomposed and putrefying samples contained relatively more nitrogen than the first stages. This increase in the quantity of nitrogen may be occasioned by a greater destruction of the non-nitrogenous substances than of the nitrogenous matter, or by a fixation of inorganic nitrogen, or possibly by both together.

In order to determine the total quantity of detritus and plankton, a series of filtrations of sea water were made at Nykøbing Mors by cand. Grøntved. Water samples from Sallingsund were (with the exception of a single sample) found to contain a far greater amount of detritus than of plankton organisms. The weight of dry matter in the residue varied between 9,6 and 72,3 mgr. per 10 L. of the sea water. No relation could be shown to exist between the weather conditions and the amount of detritus in the water.

Investigations were also made with a view to ascertaining how far digestible matter could be shown to exist in the sea bottom. The amount of nitrogenous matter digestible with pancreatin was comparatively small; the values found are probably only minimal figures. The investigations of Biedermann and Moritz lead us to believe that bivalves are capable of digesting pentosan, which, as already mentioned, is found in the sea bottom in considerable quantities.

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VII. Tables.

Tab. 12. Zostera, determination of carbon and organic matter.

	Quantity examined gr.	Amount of dry matter gr.	Amount of CO_2 found gr.	Amount of C calculated gr.	% of C in the dry matter	Amount of ash found gr.	% of organic substances in the dry matter
Green *Zostera*, Nyborg Fjord $^{11}/_{2}$ 13	0,5	0,404	0,500	0,137	33,9	0,108	73,8
Brown *Zostera*, Nyborg Fjord $^{11}/_{2}$ 13	0,5	0,433	0,485	0,133	30,7	0,113	74,0
Dead weed, Nyborg Fjord $^{11}/_{2}$ 13	0,5	0,428	0,522	0,142	33,0	0,100	76,5
Brown *Zostera*, Svendborgsund 1912	0,5	0,5	0,533	0,146	29,2		
Fine *Zostera*, S. of Grenaa harbour, $^{28}/_{4}$ 13	0,5	0,472	0,508	0,139	29,6	0,164	65,2

Tab. 13. Zostera, determinations of pentosan.

	Quantity examined gr.	Amount of dry matter gr.	Amount of floro-glucid found	Amount of pentosan calculated	% of pentosan in the dry matter
Green *Zostera*, Nyborg Fjord $^{11}/_{2}$ 13	2,5	2,020	0,185	0,169	8,4
Brown *Zostera*, Nyborg Fjord $^{11}/_{2}$ 13.....	2,5	2,165	0,199	0,181	8,4
Dead weed, Nyborg Fjord $^{11}/_{2}$ 13.....	2,5	2,140	0,177	0,162	7,6
Brown *Zostera*, Svendborgsund 1912	2,5	2,5	0,206	0,187	7,6
Fine *Zostera*, S. of Grenaa harbour $^{28}/_{4}$ 13....	2,5	2,360	0,163	0,149	6,3

Tab. 14. Plankton, determination of carbon and organic matter.

	Quantity of dry matter examined gr.	Quantity CO_2 found gr.	Amount C calculated gr.	% of C in the dry matter	Quantity examined gr.	Amount of ash found gr.	% of organic substances in the dry matter
Chætoceras plankt., The Sound $^{31}/_{5}$ 11.....	0,2	0,075	0,0205	10,25			
Peridinean plankt., Svendborgsund $^{8}/_{10}$ 13.....	0,2	0,161	0,044	22,0			47,0
Copepod- and peridinean plankt., Fænø Sund $^{16}/_{8}$ 13	0.2	0,1035	0,0282	14,1			
Chætoceras plankton, oyster basin, Nykøbing M. $^{20}/_{7}$ 13	0,2	0,0810	0,0220	11,0			
Chætoceras plankton, oyster basin, Nykøbing M. $^{22}/_{7}$-$^{14}/_{8}$ 13	0,2	0,0855	0,0233	11,7	0,2949	0,2146	27,2

Tab. 15. Plankton, determinations of pentosan.

	Quantity examined gr.	Amount of floro-glucid found	Calculated amount of pentosan	% of pentosan
Chætoceras plankton, The Sound $^{31}/_{5}$ 11	5	0,030	0,0315	0,63
Peridinean plankton, Svendborgsund $^{8}/_{10}$ 13	1	0,0085	0,0122	1,22
Copepod- and peridinean plankton, Fænø Sund $^{16}/_{8}$ 13	1,179	0,0154	0,018	1,52
Chætoceras plankton, oyster basin, Nykøbing M. $^{20}/_{7}$ 13	2,2	0,020	0,0225	1,02
Chætoceras plankton, oyster basin, Nykøbing M. $^{22}/_{7}$—$^{14}/_{8}$ 13	2	0,0225	0,0247	1,24

Tab. 16. Bottom samples: determinations of carbon.

	Quantity examined gr.	Amount of CO_2 found gr.	Calculated amount of C gr.	% of C
Nyborg Fjord, upper layer, 16,5 m, $^{21}/_{10}$ 12	5	0,425	0,116	2,3
Nyborg Fjord, upper layer, washed, 21 m, $^{24}/_{9}$ 13	5	0,993	0,270	5,4
Detritus, Thisted Bredning, 1910	4,0272	0,4415	0,1125	2,8
Livø Bredning, off Ørodde, upper layer, 1912	5	0,685	0,187	3,7
Livø Bredning, upper layer from various oyster beds, $^{9}/_{9}$ 13	3	0,228	0,062	2,1
Kattegat, N. of Fune, upper layer, $^{20}/_{6}$ 12	2	0,405	0,110	5,5
Kattegat, E of St. Middelgrund, 1911	5	0,463	0,126	2,5

Tab. 17. Bottom samples: determinations of pentosan.

	Quantity examined gr.	Amount of floro-glucid found	Calculated amount of pentosan	% of pentosan
Nyborg Fjord, upper layer, 16,5 m, $^{21}/_{10}$ 12	20	0,089	0,0838	0,42
Nyborg Fjord, upper layer, washed, 21 m, $^{24}/_{9}$ 13	20	0,182	0,1660	0,83
Detritus, Thisted Bredning, 1910	20	0,105	0,0979	0,49
Livø Bredning, off Ørodde, upper layer, 1911	20	0,107 0,120	0,1055	0,53
Livø Bredning, upper layer from various oyster beds, $^{9}/_{9}$ 13	10	0,026	0,028	0,28
Kattegat, N. of Fune, upper layer, $^{20}/_{6}$ 12	10	0,114	0,1059	1,06
Kattegat, E of St. Middelgrund, 1911	20	0,060	0,0581	0,29

Tab. 18. Zostera samples, Nyborg Fjord, January 1913. Determinations of organic matter and carbon.

	Quantity examined gr.	Quantity of dry matter gr.	Amount of ash found gr.	% of organic substances in the dry matter	Amount of CO_2 found gr.	Calculated amount of C gr.	% of C in the dry matter
1.	0,5	0,404	0,108	73,8	0,500	0,137	33,9
2.	0,5	0,485	0,120	75,2	0,613	0,168	34,6
3.	0,5	0,458	0,112	75,8	0,570	0,155	33,8
5.	0,5	0,433	0,113	74,0	0,485	0,133	30,7
7.	0,5	0,470	0,129	72,8	0,544	0,149	31,8
9.	0,5	0,444	0,192	56,8	0,461	0,126	28,5
10.	0,5	0,428	0,100	76,5	0,522	0,142	33,0

Tab. 19. Zostera samples, Nyborg Fjord, January 1914. Determinations of nitrogen.

	Quantity examined gr.	Quantity of dry matter gr.	Amount of N found gr.	% of N in the dry matter
1.	0,5	0,404	0,0120	2,97
2.	0,5	0,485	0,0099	2,05
3.	0,5	0,458	0,0050	1,10
5.	0,5	0,433	0,0038	0,88
7.	0,5	0,470	0,0054	1,16
9.	0,5	0,444	0,0044	0,99
10.	0,5	0,428	0,0060	1,39

Tab. 20. Zostera samples from Nyborg Fjord, $^{24}/_{9}$ 13. Determination of organic matter.

	Quantity examined gr.	Quantity of dry matter gr.	Amount of ash found gr.	% of organic substances in the dry matter
1.	0,5	0,4935	0,135	72,6
2.	0,5	0,4405	0,137	69,0
3.	0,5	0,4785	0,169	64,6
4.	0,5	0,4915	0,223	54,5

Tab. 21. Zostera samples from Nyborg Fjord, $^{24}/_{9}$ 13. Determination of nitrogen.

	Quantity examined gr.	Quantity of dry matter gr.	Amount of N found gr.	% of N in the dry matter
1.	0,5	0,4935	0,0067	1,35
2.	0,5	0,4405	0,0054	1,23
3.	0,5	0,4785	0,0055	1,15
4.	0,5	0,4915	0,0065	1,33

Tab. 22. Zostera, Limfjord, W. of Mors, $^{21-23}/_{7}$ 13.
Determination of organic matter.

	Quantity examined gr.	Quantity of dry matter gr.	Amount of ash found gr.	% of organic substances in the dry matter
1.	0,5	0,462	0,0952	79,4
2.	0,5	0,449	0,1816	59,5
3.	0,5	0,468	0,2320	50,5
4.	0,5	0,462	0,2060	55,3

Tab. 23. Zostera, Limfjord, W. of Mors, $^{21-23}/_{7}$ 13.
Determination of nitrogen.

	Quantity examined gr.	Quantity of dry matter gr.	Amount of N found gr.	% of N in the dry matter
1.	0,5	0,462	0,00385	0,83
2.	0,5	0,449	0,0028	0,62
3.	0,5	0,468	0,0031	0,66
4.	0,5	0,462	0,0044	0,95

Tab. 24. Zostera samples, Nykøbing, Mors, Bugt. $^{12}/_{9}$ 13.
Determination of organic matter.

	Quantity examined gr.	Quantity of dry matter gr.	Amount of ash found gr.	% of organic substances in the dry matter
1.	0,5	0,4875	0,1338	71,6
2.	0,5	0,4900	0,1627	66,8
3.	0,5	0,4620	0,1160	74,8
4.	0,5	0,4905	0,2000	59,1

Tab. 25. Zostera samples, Nykøbing, Mors, Bugt. $^{12}/_{9}$ 13.
Determination of nitrogen.

	Quantity examined gr.	Quantity of dry matter gr.	Amount of N found gr.	% of N in the dry matter
1.	0,5	0,4875	0,00712	1,46
2.	0,5	0,4900	0,00345	0,71
3.	0,5	0,4620	0,00445	0,96
4.	0,5	0,4905	0,00730	1,49

Food and Conditions of Nourishment among the communities of invertebrate animals found on or in the sea bottom in Danish waters.

By

H. Blegvad,

cand. mag., Assistant at the Danish biological Station.

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The present investigations*) have been carried out with freshly collected material on board the s/s »Sallingsund« belonging to the Danish Biological Station. The contents of the stomach was removed immediately after capture, and thereafter analysed with lens or microscope. In addition, the nourishment of various species was studied in small glass aquaria with a layer of detritus at the bottom, observations being made at the same time as to the manner in which these animals took in their food. The object of this was primarily to furnish some contribution towards the study of the metabolism of the sea, and special efforts have therefore been made to discover the main food of the commonest and most widely distributed bottom organisms in the various communities (50, p. 5 ff.). In previous investigations of this nature, the results have been, as a rule, given only in the form of a list of names of the animal and plant species, of which remains have been found in the stomachs of the specimens investigated. This has frequently led to erroneous conclusions. In the first place it has been found that the matter as taken from the bottom layer may often already contain skeletal parts of various animals, in addition to which, those plankton animal species which are only rarely eaten, and that in but small quantities, by one or another organism, or had been accidentally devoured together with others, appear on the list as of equal importance to those of more general occurence.

In order to avoid these errors I have, for each of the analyses made as to contents of stomach and intestines (published *in extenso* as appendix to the Danish edition of the present work) noted what fraction of the total contents was furnished by each of the separate components. If a sufficient number of such quantitative observations be made, we thereby obtain an idea as to what constitutes

*) Being extract of the paper »Undersøgelser over Næring og Ernæringsforhold hos Havbundens invertebrate Dyresamfund i danske Farvande« published in Beretning Nr. XXII fra den danske Biologiske Station, Copenhagen 1914.

the principal food of the animal in question. This is frequently found to vary in a high degree according to the age of the specimen, and the place where it was found; on the whole, however, we may assert that there are three main sources of nourishment for the bottom fauna of the sea: 1) Plants, 2) Detritus and 3) Animals.

1) By **Plants** I understand fresh, growing plants of the benthos formation. As far as the Danish waters are concerned, it is especially the *Zostera* and its attendant microflora which we have here to consider. C. G. Joh. Petersen (51) has calculated that this plant produces, in leaves alone, 8232000 kg. annually in the Danish waters east of the Skaw. In course of time, these plants of the benthos formation die, or are torn away by the currents or the action of the waves, and carried out, in whole pieces or fine particles, into the deeper water, where they are deposited on the bottom in the form of detritus.

2) By **Detritus** I understand such dead or dying (decomposing) organisms or portions of same, whether of vegetable or animal origin, as are found in suspension (or solution) in the sea water or deposited on the bottom. If a fine plankton net be drawn through the water in the *Zostera* region, it is soon filled with the detached fragments of plants, both fresh and decomposed, which float about in the water. This form of detritus I have termed plant-detritus. In contrast to this the bottom detritus, as it is found deposited on the sea bottom, but rarely contains fresh fragments of vegetable matter.

3) By **Animal food** or **Carneous food** I understand all living animals found in the sea, together with their carrion, save where these are to be reckoned as forming part of the »detritus« as defined above.

That plankton is not included as a principal source of nourishment is due to the fact that the only plankton organisms which, according to my investigations, are of direct importance to the fish and bottom fauna in the Danish waters are the pelagic Crustacea and the pelagic larvæ of the bottom fauna itself, which forms are naturally comprised under the head of animal food. Many writers (e. g. Lotsy (36), Moore (43 and 44), Redeke (56), Murray (46), and Rauschenplat (55), have expressed the opinion that the phytoplankton organisms, especially the diatoms, are of extremely great importance as a food-supply for the bottom fauna, and have even reckoned bivalves and ascidians for instance as »plankton eaters«. This is, however, due to the fact that the writers in question have only taken into consideration the phytoplankton found in small quantities in the stomachs, entirely disregarding the significance and value as nourishment of the detritus simultaneously found there. This they have merely described as »sand and clay« or »unrecognisable matter«. As early as 1871, before the term »plankton« was known, Møbius wrote (Zeitschr. f. wiss. Zool. XXI) that the food of the bivalves consisted of »Moderteilchen der toten Pflanzen«. Later on, however, when the study of plankton, with Hensen (24) at the head, and with scientists like Brandt and Apstein likewise at work upon the subject, had begun to forge ahead, every thing was attributed to the plankton as the prime source of nourishment. That detritus really is a substance of importance as a food supply for many animals is, however, a point which has of late been again brought forward by a number of writers, as for instance Frenzel (19), P. P. C. Hoek (26), Rauschenplat (55),

but in particular C. G. Joh. Petersen and P. Boysen Jensen (49), who have further shown that in our waters it is the plants of the benthos formation, and not the plankton organisms, which form the principal source of the organic matter in the detritus layer of the sea bottom, and in the detritus held in suspension in the sea water. And the principal conclusion of the present investigations is, that the great majority of the bottom fauna in our waters live on detritus, none on pure phytoplankton. That the mass of detritus in the contents of the stomach really is the main source of nourishment and not the small amount of phytoplankton which may now and then be found therein, is borne out, not only by the quantitative proportion, but also by the fact that many of these plankton organisms can pass through the intestines of the animals in question without suffering any change at all; in the case of *Prorocentrum micans*, for instance, aquarium experiments have proved beyond doubt that this organism can pass through the intestines of *Ostrea edulis* and *Mytilus edulis* and even emerge alive.

With regard to the theory advanced by A. Pütter (54), to the affect that the carbon compounds present in solution in the sea water should be of very extensive importance as food for certain animals of the bottom fauna, it will here suffice to say that this must for the present be regarded as unproved, and requiring closer investigation. Pütter has, in his calculations as to the amount of water necessary to the food consumption of various animals, disregarded the detritus suspended therein, only considering the quantity of plankton organisms contained. Moreover, the fact that many animals such as Planariæ, Nemerteans and Pantopods are most frequently found with perfectly empty alimentary canal cannot be taken as proving that they derive their nourishment from dissolved matter; as will subsequently be shown, this applies to nearly all the carnivores, and is doubtless merely an indication of the fact that these animals only secure their prey at long intervals. It is very possible, however, that certain of the small detritus-eating forms can, in addition to detritus, also live on dissolved organic matter; I have therefore, for the sake of convenience, also included dissolved matter under the definition of detritus.

The enormous importance of the food value of detritus in the metabolism of the sea will be easily evident from the following survey of the commonest animal forms in Danish waters:

1) Herbivores are, first of all, the small gastropods of the vegetation region: *Rissoa membranacea* and *R. inconspicua. Cerithium reticulatum, Hydrobia ulvæ, Trochus cinerarius, Lacuna divaricata, Littorina rudis, L. tenebrosa, L. obtusata, Chiton, Tectura virginea* and *T. testudinalis;* in addition to their vegetable food, however, the small gastropods also devour detritus, especially plant-detritus. The same applies to *Nereis diversicolor,* the intestines of which may contain fresh plants, plant-detritus and bottom detritus. These animals must therefore be called plant- and detritus eaters. Other gastropods such as *Littorina littorea* and *Acera bullata* are besides being plant and detritus eaters, also carnivores; the same applies to *Nereis pelagica*, two Echinoderms, viz. *Echinus miliaris* and *Strongylocentrotus drøbakiensis,* as well as a number of Crustacea: *Palæmon Fabricii, Palæmon squilla, Crangon vulgaris,* a number of *Mysidae,* Amphipods, and Isopods. Herbivorous and carnivorous are

only some larger crustaceans viz. *Carcinus mænas, Hyas coarctatus, Stenorhynchus rostratus* and possibly *Homarus vulgaris.*

2) Pure Detritus eaters are firstly, all the Lamellibranchs which I have examined, as well as the *Spatangidæ*, Holothurians, *Sipunculidæ, Cumacea, Diptera* larvae and *Ascidiæ;* the two gastropods *Turritella terebra* and *Aporrhaïs pes pelecani,* and in addition, *Chætoderma nitidulum,* most of the *Polychæta, Echiurus Pallasii, Balanoglossus Kuppferi, Amphioxus lanceolatus, Amphiura Chiajei, A. filiformis,* some amphipods, and doubtless all Ostracods, bottom copepods, *Bryozoa, Porifera* and *Foraminifera.* That these animals really live on detritus is evidenced partly by direct observation in a natural state and in aquaria, partly by the fact that the contents of their stomach and gut forms a mass which on microscopic examination is found to agree entirely with the detritus layer of the sea floor and the mass of detritus held in suspension near the bottom. We find the same components, not always, however, in the same proportions. The reason of this is that many detritus eaters are able to sort out the coarser, useless particles from the remainder before passing the mass into the alimentary canal. This is especially the case with bivalves, ascidians and crustaceans; most worms, however, as also *Brissopsis* and *Echinocardium,* take in the detritus of the bottom without any selective process.

Table 1.

	gr. dry matter	% of Nitrogen
Modiola modiolus, 110 specimens, SW. of Helsingborg, 30 m. $^{13}/_{8}$ 1912:		
Contents of stomach	0,221	9,3
» » intestines	0,134	1,66
Mytilus edulis, Thisted Bredning $^{1}/_{8}$ 1912:		
Contents of stomach	0,145	2,68
Fæces	0,130	0,69
Ostrea edulis, The Limfjord 1912:		
Fæces	—	1,65
Cyprina islandica, Gt. Belt St. 6, E. of Vresen, $^{28}/_{6}$ 1913:		
Contents of intestines	0,0444	2,24
Upper layer of bottom same place	—	0,367
Ciona intestinalis, 350 gr. rough weight, Isefjorden (Nykøbing Bugt) 18—19. August 1913:		
Fæces, secreted in 20 hours	0,1642	1,56
Phallusia aspersa, 475 gr. rough weight, Venø Bugt $^{22}/_{7}$ 1913:		
Fæces, secreted in 6 hours	0,1355	0,94
Upper layer of bottom same place	—	0,25
Arenicola marina, Slipshavn, Nyborg Fjord $^{22}/_{2}$ 1913:		
Fæces	5,0	0,013
Upper layer of bottom	5,0	0,033
Arenicola marina, Nyborg Fjord $^{3}/_{10}$ 1913:		
Fæces	5,0	0,029
Upper layer of bottom	5,0	0,029
Arenicola marina, Blødens Pæle $^{10}/_{9}$ 1913:		
Fæces	5,0	0,025
Upper layer of bottom	5,0	0,027
Arenicola marina, Hals $^{10}/_{9}$ 1913:		
Fæces	5,0	0,016
Upper layer of bottom	5,0	0,043

	gr. dry matter	% of Nitrogen
Arenicola marina, Nyborg Fjord $^{18}/_{12}$ 1913:		
Fæces	12,8	0,0207
Upper layer of bottom	12,8	0,0234

This is most distinctly shown in Table 1, giving the results of a number of quantitative analyses for percentage of nitrogen in the contents of the stomach of various animals. We find that the percentage of nitrogen in the contents of stomach and fæces of bivalves and ascidians is far higher than that of the upper detritus layer of the bottom at the same locality, whereas the percentage of nitrogen in the fæces of *Arenicola marina* is always below that of the bottom. Thus for instance, the percentage of nitrogen in the fæces of *Phallusia aspersa* is 0.94, that of the bottom being 0.25. The fæces of *Arenicola* on the other hand, contain for instance 0,013 % of nitrogen, the corresponding figure for the adjacent bottom being 0.033.

Thus the bivalves and ascidians are able in a very high degree to condense the nitrogen contained in the bottom; this is done primarily by the fine sorting of the detritus. Possibly also, the process of digestion chiefly affects the non-nitrogenous compounds therein contained, and finally, as already mentioned, a number of organisms are passed entirely unchanged through the digestive organs of the animals in question. All this serves to explain the remarkably high percentage of nitrogen still remaining in the excrements of the bivalves and ascidians in Table 1.

The intestines of detritus eaters are almost invariably found to contain, in addition to detritus, some few plankton forms, these being, however, as a rule but a small fraction of the total contents. Only in a very few cases have I found the quantity of plankton to exceed that of the detritus in the digestive organs, and this has always proved to be but a phenomenon of brief duration. In Thisted Bredning for instance, on the 13.—15. Sept. 1913, all the larger bivalves and ascidians which live on suspended detritus (e. g. *Mytilus edulis, Ostrea edulis, Mya truncata, Saxicava rugosa, Cyprina islandica* and *Ciona intestinalis*) had stomach and intestines full of the silicoflagellate *Distephanus speculum*, practically all, however, being merely skeletons, and amounting to about $^3/_4$ of the contents, with a quantity of *Prorocentrum micans*, and only very little detritus. The smaller bivalves, however, *Abra alba* and *Nucula nitida*, which suck up directly the particles of the uppermost bottom layer itself, had very few, if any, of either *Distephanus* or *Prorocentrum* in the stomach. On making the next investigations, two days later, (on the 17th of Sept.) the large bivalves above mentioned were already found to again contain more detritus than plankton. The *Distephanus*, which was practically only present in skeleton form, cannot have been of any importance as food for the animals in question. A bottom-sample taken with a glass tube showed that most of the *Distephanus* floated in the water a little above the bottom, only comparatively few being found on the bottom itself. This explains the small quantity of *Distephanus* found in the *Abra* and *Nucula* The many millions of

suspended *Distephanus* skeletons must have filled the bottom water to such an extent that the large bivalves and ascidians, living as they do on suspended detritus could not avoid swallowing some of them.

In *Psolus phantapus* and *Phyllophorus pellucidus* also, I have only exceptionally found *Chætoceras* and *Rhizosolenia* in considerable quantities, and here likewise only empty cells. On the other hand, many of those bivalves which, like *Mytilus edulis*, often live high up in the water, are able to sort their food, discarding most of the larger plankton organisms, so that even when the water is full of *Chætoceras* or *Ceratium*, these forms are only very rarely found in the contents of the stomach.

The living phytoplankton is thus of no importance at all as food for the bottom fauna; even for the plankton fauna itself it would seem, according to Dakin (9) and Lohmann (33, p. 275; 34, p. 72 and 35, p. 99) that only the very smallest forms and the ubiquitous detritus are of any significance in this respect. It is therefore entirely erroneously that G. Murray (46, p. 211) after having referred to the finding of diatoms in Holothurians, Ascidians, *Salpæ*, oysters scallops, gastropods and other molluscs, crabs, lobsters and other large crustacea (!) or even in full grown fishes, concludes by observing that diatoms and other pelagic algae form the basis of nourishment for all marine animals, and are »the pastures of the sea«.

Not until the plankton algae sink to the bottom and die — i. e. become detritus — are they of any importance to the bottom fauna. It is quite a different matter, however, with the sessile diatoms which are found growing on algae, stones and wood, and are often scraped off in great quantities by the herbivorous gastropods; also, perhaps, with the bottom diatoms, which are devoured together with the upper detritus layer by the detritus eaters. Many of the bottom diatoms appear, it is true, to pass entirely unchanged through the digestive organs of the consumer, presenting as a rule exactly the same appearance when encountered in the posterior portion of the intestines as in the anterior. Moreover, the bottom diatoms are scarcely ever found except in comparatively small quantities, and therefore doubtless as merely accidental components, mixed with the detritus in the stomach and intestines of detritus eaters. The sessile diatoms, on the other hand, are very often found almost unmixed in the intestines of gastropods, for instance *Littorina littorea* and *Rissoa membranacea*.

3) Purely carnivorous are only some few *Polychæta*, some gastropods, *Neptunea antiqua*, *Buccinum undatum*, *Nassa reticulata*, the *Natica*-species, and *Bela turricula*, with *Portunus depurator*, *Hyas coarctatus*, *Inachus dorsettensis*, and *Echinus esculentus*. In addition, all the *Asteroidea* and *Actiniidæ* investigated, and possibly all *Hydroidæ*, nemerteans, *Planariæ* and pantopods. Finally, a large number of animals are simultaneously carnivores and detritus-eaters: *Ophiopholis aculeata*, *Ophiothrix fragilis*, and the *Ophioglypha* species, Nudibranchs, *Philine aperta*, *Dentalium entalis*, *Priapulus caudatus*, *Halicryptus spinulosus*, *Moera Lovenii*, *Mysis mixta*, *Gastrosaccus spinifer*, *Crangon Allmani*, *Pandalus montagui*, the *Eupagurus*-species, possibly *Calocaris Macandreae* and *Echinocyamus pusillus*.

These animals can be divided into natural groups according to the arrangement of the organs with which they secure and devour their food, the groups

thus formed being also, it has been found, closely connected as regards the selection of the food in question. As will be seen from the tabular scheme below, we obtain two main divisions viz, those without and those with hard prehensile or masticatory organs. In the first main group, subdivision commences with the most primitive method of taking in the food, viz, by means of pseudopodia; then comes the more complicated cilia system, leading again to the organisms with tentacles, extroversible gullet, and ambulacral feet (tube-feet). The animals included in the former categories are all pure detritus eaters; in this last group, however, (those which take in nourishment by means of ambulacral feet) we further find some which are both carnivores and detritus eaters, and finally, the animals with nematocysts are found to be all exclusively carnivorous. The next main group, of animals with hard prehensile or masticatory organs, includes detritus eaters, carnivores, and »mixed feeders«; these I have divided into four large groups, according as they are furnished with radula, mandibulated gullet, chitine-covered limbs, or calcareous teeth. It should here be noted, that in cases where I have not been able to personally investigate the manner of feeding, the statements as to food of the animal in question have been placed in parenthesis.

A. Animals without hard prehensile or masticatory organs.

I. Those feeding entirely by means of pseudopodia: *Foraminifera* (Detritus eaters).

II. Those feeding by means of a ciliate epithelium occasioning a constant current of water through a portion of their body.

a) without gills: *Porifera* (Detritus eaters).

b) with gills serving as a selective filter:

1. *Lamellibranchia* .....
2. *Ascidiæ* ..... } Detritus eaters.
3. *Amphioxus lanceolatus* .....

III. Those feeding by means of prehensile arms or tentacles without nematocysts but frequently furnished with cilia:

1. Various *Polychæta: Chloræmidæ, Amphictenidæ, Ampharetidæ, Terebellidæ, Sabellidæ, Serpulidæ.* ..... } Detritus eaters.
2. *Holothurioidea* .....

IV. Those feeding by means of a soft, generally extroversible gullet, or proboscis, for drawing up the detritus of the bottom:

1. Various *Polychæta: Telethusæ, Ariciidæ, Opheliidæ, Scalibregmidæ, Capitellidæ, Maldanidæ.* .....
2. *Sipunculidæ* ..... } Detritus eaters.
(3. *Echiurus Pallasii* .....
4. *Balanoglossus Kuppferi)* .....

V. Those feeding by means of ambulacral feet (tube-feet):

1. *Echinoidea irregularia* without masticatory organs = *E. atelostomata.* ..... } Detritus eaters.
2. *Amphiura Chiajei, A. filiformis* .....

3. The remaining *Ophiuroidea* Carnivorous detritus eaters.
4. *Asteroidea* ..... Carnivores.

VI. Those feeding by means of prehensile tentacles furnished with nematocysts:

1. *Actiniidæ* .....
(2. *Hydroidæ*) ..... } Carnivores.

B. Animals with hard prehensile or masticatory organs.

I. Those feeding by means of a radula:

Mollusca glossophora ..... { Detritus eaters. Herbivorous detritus eaters. Herbivorous and carnivorous detritus eaters. Carnivorous detritus eaters. Carnivores.

II. Those feeding by means of an extroversible gullet, furnished with hard mandibles or teeth:

1. Various *Polychæta: Aphroditidæ, Polynoidæ, Acoëtidæ, Lycoridæ, Lumbrinereidæ, Glyceridæ, Goniadidæ, Nephthydæ* ..... { Herbivorous detritus eaters. Carnivorous and herbivorous detritus eaters. Carnivores.
2. *Priapulidæ* ..... Carnivorous detritus eaters.

III. Those feeding by means of setæ-covered limbs with chitinous cuticle, generallly also having a masticatory stomach furnished with chitinous plates:

1. *Crustacea.* ..... { Detritus eaters. Herbivorous detritus eaters. Herbivorous and carnivorous detritus eaters. Carnivorous detritus eaters. Carnivores.
2. *Diptera larvæ* ..... Detritus eaters.

IV. Those feeding by means of a masticatory organ with 5 calcareous teeth:

Echinoidea regularia and *E. irregularia* with masticatory organs = *E. gnathostomata.* { Carnivorous detritus eaters. Herbivorous detritus eaters. Carnivores.

A. Animals without prehensile or masticatory organs.

I. Those feeding exclusively by means of pseudopodia:

Foraminifera.

These small organisms sometimes play a not unimportant part as food for other animals. *Philine aperta* and *Dentalium entalis* for instance, pick them up from the detritus layer of the bottom. According to O. Bütschli (Dr. H. G. Bronn's Klassen u. Ordnungen des Thier-Reichs. Protozoa) the *Rhizopoda* live upon diatoms, *Protococci* and similar forms, some few animals (mostly unicellular) but also detritus and portions of polycellular plants, principally algæ. As regards

the Foraminifera of the sea bottom, the detritus will be of especial importance among these food stuffs, since it is found in abundance where these animals live, whereas the plants and plankton organisms are only encountered by them when already dead, i. e. in the form of detritus.

II. Animals feeding exclusively by means of a ciliate epithelium, occasioning a constant current of water through a portion of their body.

a. Without gills.

Porifera. (3 specimens examined from 2 different localities.)[1])

By squeezing the water from sponges I have always found a quantity of detritus with *Prorocentrum*, small peridineans, bottom diatoms and Foraminifera. That the sponges are true detritus eaters is shown by the fact that they are obliged, like the other true detritus eaters, the bivalves and ascidians, to take their food from the water which is continnally passed through them by the action of the ciliary cells. In this water, detritus is, as already mentioned, the principal source of nourishment. This agrees with what E. Haeckel (Die Kalkschwämme, Bd. I, Berlin 1872, p. 372—74) writes: that the calcareous sponges live mainly on decomposing animal and vegetable matter, possibly however, also on dissolved substances and micro-organisms. I have only found sponges in the stomach of *Lepidonotus squamatus* and *Nereis pelagica;* Rauschenplat (55) has found portions of *Amorphina panicea* in *Littorina littorea*. *Ophiopholis aculeata* and *Ophiothrix fragilis*, which frequently select sponges as their place of residence, do not eat them; there is never any trace of them in their stomachs.

b. With gills serving as selective filter.

1. *Lamellibranchia.*

All the bivalves which I have examined are without exception true detritus eaters. As already mentioned, they are all able to sort through the detritus; this sorting process, however, can be more or less finely selective, and it has been found possible to distinguish between two great groups of bivalves: the roughly-sorting and the finely sorting. Closer examination of the feeding of these animals has moreover shown, that the first group consists of animals which sit with outstretched, motionless siphons, or have no siphons at all, and feed exclusively on such suspended detritus as is carried by the constant current of water towards their gills. This first group can again be subdivided into two, according as the

[1]) With regard to the figures in brackets here and in the following placed after the name of each animal as indicating the number of investigations of contents of stomach and intestines, these represent, especially in the case of detritus eaters, only such investigations as have been recorded with statements of time, place, quantitative proportion of components, etc. (published with all details in the danish edition of this report). As a matter of fact, the number of specimens actually investigated is in every instance far greater; these investigations however, having given exactly identical results, have therefore not been recorded. In the course of these investigations, moreover, experience has shown that a single examination, or a very few such, will as a rule suffice to determine whether any particular animal is a detritus eater; when the alimentary canal is each time found to be stuffed with pure detritus, we may safely presume this to be the case. A great number of specimens must be examined however, in order to determine what a carnivorous animal feeds on.

bottom detritus is drawn up by means of siphons, which are then long and separate, or by a labial palp appendage.

We have thus three groups in all:

1) Bivalves with long, separate siphons, and no labial palp appendages.

Abra (Syndosmya) alba Wood	(13 specimens examined, from 8 different localities).
» » *nitida* Müller	(3 » »).
» » *prismatica* Mtg.	(2 » »).
Macoma calcarea Chemn.	(17 » » from 6 different localities).
» *baltica* L.	(13 » » » 6 » »).
Tellina fabula Gronovius	(2 » »).
» *tenuis* D. C.	(5 » » from 3 different localities).
Scrobicularia piperata Gmelin.	(1 » »).

These animals, all of which I have studied in aquaria, take in their food by means of the branchial siphon, which is capable of very considerable extension

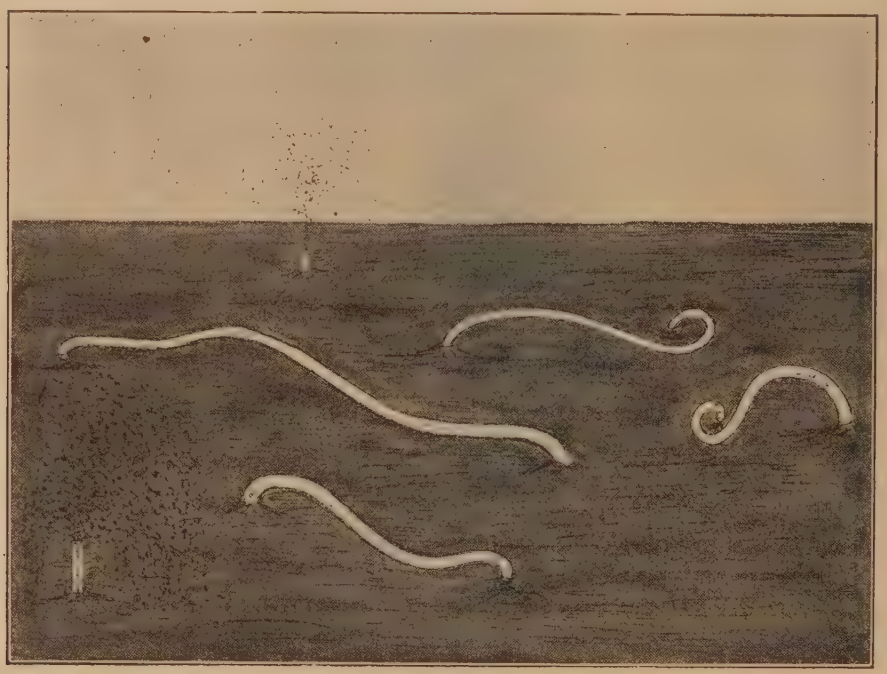

Fig. 1.
Macoma calcarea in aquarium, feeding by means of siphons. Natural size.

(in the case of large *Macoma calcarea* often nearly 10 cm) and operates in a manner similar to that of an elephant's trunk, its free end moving hither and thither in search of food, and now and then detaching a small particle of detritus from the bottom; this is then carried through the siphon by means of ciliary movement in the same down to the animal itself, which sits buried deep in the ooze (Fig. 1). When a certain quantity of detritus has been absorbed, the siphon

contracts, and a moment later a slight eruption takes place, a cloud of detritus being suddenly ejected from the contracted siphon (see Fig. 1). It is evidently the rejected coarser matter which the animal thus casts out.

The analyses of contents of stomach show, however, that this selective process is as a rule only rough. These animals must thus be said to feed on rougly sorted bottom detritus.

All of them are eagerly sought for as food by fish: plaice, dab, flounder, eel, *Zoarces viviparus*, and *Lumpenus*, but are also eaten by *Nephthys*, *Asterias rubens*, *Ophioglypha albida* and *O. texturata*, the larger predatory gastropods, crabs etc. *Macoma calcarea*, for instance, is also a favourite food of the diving ducks.

2) Large labial palp appendages used in feeding; where siphons are present, they are usually short or fused together.

Nucula nitida Sowb. (6 specimens examined, from 3 different localities).
» *tenuis* Mtg. (2 » »).
» *sulcata* Brown. (2 » »).
» *nucleus* L. (2 » »).
Leda pernula Müll. (6 » » , from 3 different localities).
» *minuta* Müll. (2 » » » 2 » »).

After the theory had been advanced by Mitsukuri (42) that the long and peculiar labial palp appendices of the *Nucula* must be used for feeding, since they were always found half filled with sand, Drew (15 and 16) found, by aquarium observations, that *Nucula delphinodonta* takes up its nourishment directly from the bottom by means of these (Fig. 2). I have not directly observed this in aquaria; there can however, be no doubt that the *Nucula*- and *Leda*-species above mentioned also feed in the same way, since they are all provided with similar labial palp appendices. In conformity with this, the contents of their stomachs is found to consist of roughly sorted bottom detritus. These bivalves also are devoured by fish, especially *Nucula tenuis*, which forms an important item in the food of the plaice in the Kattegat and the Belt Sea; they are also eaten by hermit crabs and star-fishes.

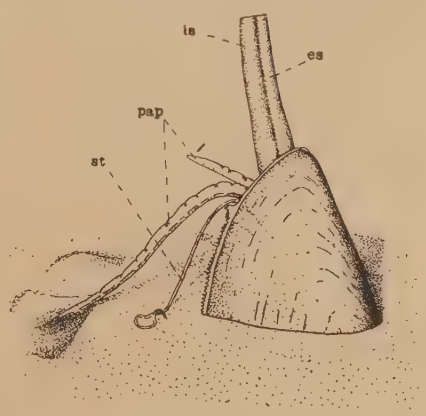

Fig. 2.
Yoldia limatula, feeding by means of labial palp appendage.
From Drew (16).
st Siphonal tentacle, *pap* labial palp appendages, *is* branchial-, *es* anal siphon.

3) When siphons are present, they are either very short or are fused together; no specially adapted labial palp appendages for feeding purposes.

Saxicava arctica L. (3 specimens examined from 3 different localities).
Mya truncata L. (15 « » » 6 » »).
» *arenaria* L. (5 » » » 2 » »).
Zirphœa crispata L. (2 » » » 2 » »).
Corbula gibba Olivi. (35 » » » 8 » »).
Thracia papyracea Poli. (1 » »).
Solen pellucidus Penn. (12 » » from 5 different localities).
Mactra subtruncata Mtg. (4 » » » 2 » »).
» *elliptica* Brown. (1 » »).
Venus gallina L. (1 » »).
» *ovata* Penn. (1 » »).
Tapes pullastra Mtg. (1 » »).
Astarte Banksii Leach. (7 » »).
» *borealis* Chemn. (9 » » from 2 different localities).
» *elliptica* Brown. (2 » » » 2 » »).
Cyprina islandica L. (15 » » » 8 » »).
Cardium echinatum L. (1 » »).
» *edule* L. (6 » » from 5 different localities).
Axinus flexuosus Mtg. (10 » » » 3 » »).
Montacuta ferruginosa Mtg. (2 » »).
» *bidentata* Mtg. (4 » »).
Modiolaria nigra Gray. (1 » »).
» *discors* L. (2 » »).
» *marmorata* Forb. (1 » »).
Modiola modiolus L. (19 » » from 8 different localities).
Mytilus edulis L. (156 » » » 37 » »).
Lima Loscombii Sowb. (8 » » » 3 » »).
Pecten septemradiatus Müll. (6 » » » 4 » »).
» *opercularis* L. (10 » » » 5 » »).
» *varius* L. (4 » » » 2 » »).
Ostrea edulis L. (21 » » » 10 » »).

The bivalves of this group, having no special organs for actively drawing up matter from the detritus layer of the bottom, are obliged to have recourse to that suspended in the water. This detritus is, however, as has been shown by Boysen-Jensen (49, p. 32) identical with the upper detritus layer of the bottom: i. e. a bottom detritus freed of its coarser particles by washing. A further selective process is now set in motion by the bivalves themselves, partly by means of the papillae or »tentacles« of the mantle, partly by a special ciliary arrangement, as studied by Wallengreen (Lunds Universitets Aarssk. N. F. Afd. 2. Bd. 1. No. 2—3) and Orton (48). The rejected matter is accumulated at certain parts of the mantle, and then »blown« off, by the bivalve suddenly closing its shell.

Fish, crabs, and *Asteridae* are the worst foes of these bivalves, the large *Cyprina islandica*, however, being probably only devoured by large *Asterias rubens* (and lobster?), whereas the large *Mytilus edulis* is also eaten, for instance, by eels, which are able to extract the soft parts from the shell. The cod have learned to snap off the long foot of *Cardium echinatum*, or to bite off and devour the extremities of the siphons of large bivalves such as *Mya truncata*. The smaller forms, and larvae of the larger, are eaten to a great extent by the predatory gastropods, *Buccinum*, *Nassa*, and *Natica*, as also by *Carcinus mænas* and *Paguridæ*. True detritus eaters such as *Echinocardium cordatum*, which feed on the upper layer of the bottom, also destroy annually millions of quite small and young lamellibranchs, which accidentally find their way into their intestines.

The small bivalves while in the bottom stage live on the same food as the grown individuals, the detritus being, however, more finely sifted. In pelagic lamellibranch larvae I have found a fine detritus-like mass, without visible remains of organisms.

2. *Ascidiæ.*

Ciona intestinalis L. (19 specimens examined from 8 diff. localities).
Styelopsis grossularia van Beneden } (39 specimens examined from 7
Styela rustica L. } diff. localities).
Phallusia aspersa Müll. (7 specimens examined from 4 diff. localities).
Clavellina lepadiformis Müll. (2 specimens examined).

As shown by the analyses, the alimentary canal of these animals contains a mass of detritus which is always found to be carefully sifted, presenting a strong resemblance to the contents of the intestines of bivalves belonging to Group 3. The food, which consists of suspended detritus, is also taken in a manner entirely analogous, the water immediately above the bottom being filtered through the fine mesh of the gills. Rauschenplat's »reines plankton« in the *Cynthia (Styela) rustica* and *Cynthia (Styelopsis) grossularia* (55, p. 144) has doubtless been dead plankton; a similar case to that of the previously mentioned spontaneous occurrence of *Distephanus* in Thisted Bredning or plankton diatoms in Holothurians.

The ascidians have but few enemies in the Danish waters; only in *Carcinus mænas* and *Strongylocentrotus drøbakiensis* have I found any indubitable remains of *Styela*.

3. *Amphioxus lanceolatus* (Pallas) (11 specimens examined from 3 diff. localities).

The *Amphioxus* also subsists on finely sorted detritus, the rough sorting is done by the cirrhi and the velum, the finer by the cilia in the branchial sac. The *Amphioxus* is in many places, e. g. in the Kattegat, so common as to be a favourite food of the plaice there.

III. Animals feeding by means of prehensile arms or tentacles without nematocysts but frequently furnished with cilia.

1. *Polychæta.*

1) Filiform tentacles.

Chloræmidæ { *Trophonia plumosa* Müll. (20 specimens examined from 7 diff. localities).
{ *Brada villosa* Rathke (2 » » » 2 » »).

Amphictenidæ	*Pectinaria auricoma* Müll.	(2 specimens examined).
	» *Koreni* Mgrn.	(11 » » from 6 diff. localities).
	» *belgica* Pall.	(6 » » » 2 » »).
Ampharetidæ		(3 » » » 2 » »).
Terebellidæ	*Amphitrite Johnstoni* Mgrn.	(4 » » » 3 » »).
	» *cirrata* Müll.	(1 » »).
	Terebellides Strømi Sars.	(8 » » from 7 diff. localities).
	Nicolea zostericola Ørst.	(3 » »).
	Artacama proboscidea Mgrn.	(3 » »).
	Lanice conchylega (Pall. non aut.)	(2 specimens examined).

Fig. 3.
Trophonia plumosa in aquarium, feeding by means of two tentacles.
Side view. Natural size.

All these animals feed on unsorted or only roughly sorted bottom detritus. *Trophonia plumosa* and *Terebellidæ* I have seen feeding in aquaria; the highly extensible tentacles are furnished with a ciliate longitudinal furrow on the lower side, and by means of an incessant rolling movement, with extension and contraction of the tentacles, particles of detritus are taken up one after another, and carried to the month by the cilia on the lower side. (Figs. 3 and 4.) This method of feeding is thus closely allied to that of those bivalves which actively draw up the detritus from the bottom. *Ampharetidæ* and *Pectinaria* must be presumed to feed in a similar way by means of their tentacles.

The polychæte worms referred to are preyed upon by cod, eel, plaice, dab, and *Lumpenus*. In addition, remains of *Trophonia plumosa* have been found in the stomach of *Lepidonotus squamatus* and *Lumbrinereis fragilis*, remains of *Pectinaria Koreni* in *Asterias rubens* and *Carcinus mænas*, and of *Terebellidæ* in *Aphrodite aculeata* and *Buccinum undatum*.

2) Pennate tentacles.

Sabellidæ (5 specimens examined from 4 diff. localities).

Serpulidæ { *Pomatoceros triqueter* L. (5 specimens examined from 2 diff. localities).
Hydroides norvegica Gunn. (1 » »).
Filigrana implexa Berk. (3 » »).

These live on very finely sifted detritus. The very delicately formed ciliate tentacles are excellently adapted to the purpose of taking in the detritus which floats above the bottom. When not disturbed, the *Terebellidæ* in an aquarium always sit with tentacles quietly extended. Only in dabs and in *Aphrodite aculeata* have I found remains of *Sabellidæ;* the *Echinus esculentus*, however, often feeds largely upon *Serpulidæ*, biting their tube across with its powerful teeth.

Fig. 4.
A Terebellide and 2 *Trophonia plumosa* in aquarium. The Terebellide with 7 tentacles extended, the *Trophonia* each 2. Viewed from above. Natural size.

2. *Holothurioidea.*

Phyllophorus pelludicus (Düb. & Kor.) (25 specimens examined from 11 diff. localities).
Psolus phantapus Strusf. (32 » » » 11 » »).
Synapta inhærens Müll. (2 » » » 2 » »).
Cucumaria pentactes L. (11 » » » 4 » »).

All the *Holothurioidea* examined are true detritus eaters. The two first mentioned species, which have arboriform tentacles, feed on finely sorted particles of floating detritus, which agrees with the fact that when placed in an aquarium they remain for the most part buried in the bottom, with tentacles quietly

xtended. The two last named species, on the other hand, feed on roughly sorted or entirely unsorted bottom detritus, evidently using their tentacles, like the worms, for taking up detritus directly from the bottom. This is confirmed by the observations of various writers (Quatrefages, Semon, M. Schmidt, Dohrn, F. C. Noll, E. Graeffe, Danielssen and Koren (11), Ludwig (37), Semper, Walther (64)) as to the contents of stomach and method of feeding of several *Synapta*- and *Cucumaria*-species. *Psolus phantapus* and *Phyllophorus pellucidus* I have found in the stomach of cod, *Solaster papposus* and *S. endeca* (which are capable of devouring even very large specimens of *Psolus phantapus*) as also *Lepidonotus squamatus*. *Synapta* and *Cucumaria* I have not found in the stomach of any animal.

3. *Bryozoa*.

From the nature of their alimentary organs the *Bryozoa* must also be classed under this head; their ciliate tentacles are excellently adapted to the purpose of taking in detritus, and although I have only found a mass of indeterminable matter in the stomach, it is beyond doubt that detritus forms their main source of nourishment. According to Claus-Grobben (7), the *Avicularia* of the polyps capture small organisms, which are held fast until they die and become detritus, when the residual organic matter is carried by the wash of the cilia on the tentacles in to the mouth. *Bryozoa* are only occasionally devoured by some few animals; *Nereis pelagica, Crangon, Stenorhynchus, Echinus miliaris* and *Asterias rubens*.

IV. Animals feeding by means of a soft, generally extroversible gullet or proboscis, through which they suck up the detritus of the bottom.

1. *Polychæta*.

Telethusæ:	*Arenicola marina* L.	(5	specimens	examined	from	4	diff.	localities).
Ariciidæ:	*Aricia armiger* (Müll).	(4	»	»	»	2	»	»).
Opheliidæ:	*Ophelia limacina* Rathke.	(7	»	»	»	3	»	»).
	Travisia Forbesi Johnst.	(2	»	»	»	2	»	»).
	Ammotrypane aulogaster Rathke.	(5	»	»	»	3	»	»).
Scalibregmidæ:	*Scalibregma inflatum* Rathke.	(2	»	»	»	2	»	»).
	Eumenia crassa Ørst.	(7	»	»	»	4	»	»).
Capitellidæ:	*Notomastus latericius* Sars.	(2	»	»	»	2	»	»).
Maldanidæ.		(7	»	»	»	4	»	»).

All the *Polychæta* here mentioned are true detritus eaters, swallowing the detritus of the bottom through their soft proboscis without any selective process, or at any rate only a very rough one. All live buried in the bottom, *Arenicola* and *Aricia* in waters so shallow that at ebb tide it is possible to watch them feeding. At the bottom of a little funnel-shaped depression in the sand the proboscis may be seen mowing up and down, swallowing the matter drawn down from the sides and circumference of the funnel. The vermiform excrements of *Arenicola* and *Aricia* can be seen at low tide covering miles of bottom. All the worms here

mentioned are preyed on by fish: cod, whiting, *Pleuronectidæ*, eel, *Raja radiata*, and *Asterias rubens*.

2. *Sipunculidæ* (5 specimens examined from 4 diff. localities).

The *Sipunculidæ* examined were for the most part *Phascolosoma* taken from the empty tubes of *Turritella* or *Dentalium;* all proved to be true detritus eaters. Only in *Solaster endeca* have I once found a *Sipunculide*.

3. *Echiurus Pallasii* Guèr. (2 specimens examined),

and 4. *Balanoglossus Kuppferi* Will-Suhm. (2 specimens examined),

I have, albut with some hesitation, included under this head, little being known as to their method of feeding. It is beyond doubt, however, that this takes place by means of the proboscis. Both are, moreover, decidedly detritus eaters, feeding on unsorted or roughly sorted bottom detritus. This is in conformity with the investigations of Agassiz, Bateson, and Spengel (59); the last named writer is, with Claus-Grobben (7) of opinion that the food is taken in by means of cilia on the ventral side of the head. I have found *Echiurus* in the stomach of cod, dab and eel. *Balanoglossus* I have never found in any fish: owing to its fragility, however, and the fact that it contains no easily recognisable solid skeleton parts, it might easily escape attention in a partially digested mass.

V. Animals feeding by means of ambulacral feet (tube-feet).

1. Those without arms, and living buried in the bottom.

Echinoidea irregularia without masticatory organs *(Atelostomata)*:

Brissopsis lyrifera Forb. (31 specimens examined from 6 diff. localities).
Echinocardium cordatum Pnt. (79 » » » 10 » »).
» *flavescens* Müll. (2 » »).
Spatangus purpureus Müll. (1 » »).

All these are typical detritus eaters, feeding directly on the upper layer of the bottom, without any previous sorting of the detritus. As the aquarium observations have shown, they live buried in the bottom, maintaining communication with the surface by means of vertical tubes, and drawing down their food by means of the far reaching ambulacral feet. (Described by Robertson (57), A. Hornyold Gandolfi in Biol. Ctbl. Bd. 29, 1909, and others). As already mentioned, the *Echinocardium cordatum* frequently devours, together with the bottom detritus, numbers of quite small young bivalves. Eichelbaum has, from this fact, and the presence of fragments of shells of larger bivalves, concluded that they live chiefly on lamellibranchs, which is certainly quite erroneous. The full grown *Spatangidæ* are eaten only by some few animals; I have found remains of them in large specimens of *Asterias rubens* and in the *Solaster*-species; the small *Echinocardium cordatum* however is frequently found in the stomach of dabs and plaice, and I have also found some in *Ophioglypha texturata* and in *Actiniidae*.

2. Very mobile arms; living buried in the bottom.

Amphiura Chiajei Forb. (55 specimens examined from 6 diff. localities).
» *filiformis* Müll. (208 — — — 9 — —).

The *Amphiura*-species live, as I have frequently observed in aquaria, buried deep down in the bottom, only the extremities of some of the arms reaching up over it. These extremities are in constant movement, feeling about over all the

small particles in the vicinity, and now and again coiling round and grasping some few of them, the food being then drawn down beneath the surface of the bottom to the mouth. According to Ludwig and Hamann (38), L. Cuénot has in *Amphiura squamata* found small decapods, while Wallich has in other species found Globigerina. Having noticed that *Amphiura* in aquaria would allow themselves to be fed with small pieces of meat, I was for some time inclined to believe that they might, occasionally at any rate, be carnivorous: I have, however, examined several hundreds of specimens taken at different places and seasons, without ever finding anything in their stomachs beyond more or less finely sorted bottom detritus, with the micro-organisms and skeletal parts therein contained. I am therefore of opinion that *Amphiura Chiajei* and *A. filiformis* are, in our waters, true detritus eaters. Possibly they may, like *Echinocardium cordatum*, accidentally encounter small young molluscs and pass the same into their stomach together with the detritus of the bottom, but no more. Eichelbaum (18) who has found skeletal parts in their stomachs, is of opinion that they feed on worms and many other animals; the mere presence of skeletal parts however, is, as already mentioned, no valid ground upon which to base conclusions. Both species are eaten by the common dab and long rough dab, often in considerable numbers.

3. More or less mobile arms; not living buried in the bottom.

a. *Ophiuroidea.*

Arms only slightly mobile	*Ophiothrix fragilis* Abgd.	(5 specimens examined from 2 diff. localities).
	Ophiopholis aculeata Müll.	(70 » » » 10 » »).
Arms very mobile	*Ophioglypha robusta* Ayr.	(90 » » » 9 » »).
	» *affinis* Ltk.	(13 » » » 4 » »).
	» *albida* Forb.	(144 » » » 16 » »).
	» *texturata* Link.	(306 » » » 26 » »).
	» *Sarsii* Ltk.	(1 » »).

The two first-named species, which in aquaria often sit motionless for days in their hiding places, are, in conformity with this, mainly detritus eaters; they can, however, according to Eichelbaum (18) also devour animal food. This writer has found in the contents of the stomach indubitable remains of worms (soft parts with setae still attached), crustaceans, remains of small Echinoderms and young bivalves, besides detritus.

The *Ophioglypha* species, on the other hand, which have very mobile arms, and will, in aquaria, fling themselves with astonishing rapidity and accuracy upon pieces of meat, small molluscs, and similar animal food, are distinctly carnivorous detritus eaters. They are very often found with remains of small molluscs or crustaceans in the stomach; on examining a quantity of specimens, however, a comparatively large number will always be found quite empty. Experience has shown this to be a good sign that the animal in question is carnivorous; the greater the extent to which an animal is constrained to live on prey, the greater will be the percentage found with perfectly empty stomachs, evidently on account of the length of time which frequently elapses between one capture and the next. The *Ophioglypha* species, besides animal food, eat also detritus: *O. texturata* lives, for instance, in the Limfjord, where it is found at most places in quantities (up to

71 specimens per 0.1 m²) almost entirely on detritus, as a rule with a number of large bottom diatoms. In the Kattegat, on the other hand, this species feeds chiefly on small bivalves such as *Abra alba,* small crustaceans such as *Gammaridæ, Mysidæ* and *Diastylis,* the young of *Echinocardium* and — winged insects (probably bees)! The last find indicates that they occasionably condescend to feed on carrion. — *Ophiopholis aculeata* is devoured in large quantities by cod, the *Ophioglypha* species especially by dab and long rough dab, only rarely by cod and plaice. I have, however, found remains of *Ophioglypha* in *Lepidonotus squamatus,* in *Solaster endeca, Asterias rubens, Hyas araneus, Eupagurus Bernhardus,* and *Actiniæ. Ophiopholis aculeata* also, I have found in *Actiniæ.* Finally, *Ophioglypha* occasionally devours smaller specimens of its own species.

b. *Asteroidea.* Arms slightly mobile.

Asterias rubens L.	(443	specimens	examined	from	36	diff.	localities).
Solaster papposus L.	(25	»	»	»	8	»	»).
» *endeca* L.	(8	»	»	»	3	»	»).
Astropecten Mülleri Müll. et Tr.	(55	»	»	»	11	»	»).
Cribrella sanguinolenta Müll.	(9	»	»	»	5	»	»).

All these animals are distinctly *carnivorous. Asterias rubens,* which does not, as asserted by Fürth (21, p. 165) employ the hard calcareous spines and papillae about the mouth as masticatory organs, live, in the plant region, on *Mytilus edulis,* both young and fullgrown, the small gastropods of the *Zostera* region (*Rissoa, Cerithium, Littorina, Lacuna*), *Gammaridæ, Idothea, Mysidæ,* worms such as *Spirorbis* and *Nereis pelagica,* and *Bryozoa.* On soft bottom devoid of vegetation, *Asterias* feeds on *Abra alba, Corbula gibba, Cardium fasciatum, Mytilus edulis, Cyprina islandica,* the *Venus* species, *Mactra subtruncata, Pectinaria, Ophioglypha, Echinocardium, Gammaridæ, Diastylis* etc. As regards the manner in which *Asterias* makes the large bivalves open their shells, the experiment made by Schiemenz (58) is not convincing. He has, it appears, only subjected *Asterias* to a momentary pull, *Venus verrucosa* on the other hand to a more continuous, so that his figures are not directly comparable. It would seem most probable that both poison and mechanical suction are applied when a starfish attempts to draw out a large bivalve or gastropod. In aquaria, *Asterias* exhibits extraordinary skill in getting its prey up into a corner whence it has no way of escape. In the course of two hours, an *Asterias* in an aquarium killed and devoured a large *Buccinum undatum.* No animal is safe from the attacks of *Asterias,* even fish and other starfish being devoured by them. Schiemenz (l. c.) saw two *Asterias* attack and devour an *Echinus* by forcing their bellies down into its mouth, despite its powerful teeth. Carrion also is devoured in great quantities by *Asterias,* as one may observe in aquaria and at low water. The *Solaster* species feed mainly on Echinoderms; I have found their stomachs to contain *Asterias rubens* (frequently large specimens), *Ophioglypha albida, Astrospecten Mülleri, Echinocardium cordatum* and *Psolus phantapus;* most frequently, however, these large animals are found with

empty stomachs. *Astropecten Mülleri* lives for the most part on molluscs. Small forms and young specimens especially are attacked by this voracious animal: the young of *Tellina, Venus, Mactra, Leda, Corbula, Cardium, Lucina, Cyprina, Modiolaria, Turritella* and *Natica;* small forms such as the *Crenella, Montacuta, Bela, Utriculus* and *Cylichna* species, besides *Diastylis, Ostracods,* small *Gammaridæ, Amphiuræ* and *Echinocyamus,* and Foraminifera In none of the *Asteroidea* here mentioned have I ever found any great quantity of detritus, the most one may find is a small amount originating from such detritus eaters as the animal has devoured; the devoured animals were, however, evidently carefully picked up from the bottom, even such small forms as ostracods and Foraminifera. *Cribrella sanguinolenta* I have never found with anything in its stomach, which must be taken as proof that this species, like the other *Asteroidea*, is distincty carnivorous. — The *Asteroidea* are practically worthless as food for other animals.

VI. Animals feeding by means of tentacles furnished with nematocysts.

1. *Actiniidae.*

Tealia digitata (Müll.)	(24 specimens examined from 7 diff. localities).
Tealia crassicornis (Müll.) } *Metridium dianthus* (Ell.) }	(44 » » » 7 » »).
Sagartia viduata (Müll.)	(34 » » » 2 » »).
Edwardsia chrysanthellum (Peach)	(17 » » » 3 » »).
Cerianthus Danielsseni Lev.	(9 » »).

The Actinians also are true carnivores. The food of the three first-named large forms consists as a rule of Echinoderms such as *Ophioglypha albida, O. robusta, Ophiopholis aculeata* and *Echinocardium cordatum;* in addition *Hydroidæ, Gammaridæ,* (including *Haploops tubicola*), *Balani* (Arms and soft parts), *Pycnogonidæ, Copepods* and lamellibranch larvæ; Finally, I have found indeterminable remains of ascidians or molluscs, together with the detritus excrements of such animals. *Sagartia viduata* appears to live exclusively on copepods, and lamellibranch- and gastropod larvæ. In *Edwardsia chrysanthellum* I have likewise found bivalve fry, besides ostracods and a small *Crenella,* and in *Cerianthus Danielsseni* remains of crustaceans. In the aquarium, actinians may be fed with pieces of meat, and I have seen an actinian attack and devour an *Ophioglypha albida* living in the same aquarium, and subsequently eject the indigestible calcareous skeletal parts. I have found actinians in the stomachs of cod, but never in large quantities.

(2. *Hydroidae.*

I have not personally investigated the contents of stomach in the case of the *Hydroidæ;* there can, however, be no doubt that these, like the actinians, live on animal food. This is supported by the statement of Browne (5) to the effect that a colony of *Hydroidæ* in an aquarium killed and devoured copepods

in great numbers. I have found remains of *Hydroidæ* in *Harmothoë imbricata*, *Nereis pelagica*, *Hyas araneus*, *Ophioglypha albida*, *Echinus esculentus* and *Actiniidæ*.)

VII. Planariæ and nemerteans also must be included under the heading of animals without masticatory organs; they do not however, fall under any of the group divisions quoted, and must therefore be separately dealt with. I myself have never actually found anything in the stomachs of either; according to various writers however, (Claus Grobben (7), Lang (30), Bürger (6), Punnet (53) and others) the larger nemerteans live on worms, mainly tube-building worms (*Amphitrite*, *Nephthys*, *Spirographis*, dead *Harmothoë* and *Nereis pelagica*), the smaller forms subsisting on small crustaceans. The non-parasitic *Turbellaria* are presumed to feed on small worms, *Entomostraca* and insect larvæ. They are thus all true carnivores. (Lang is, however, of opinion that *Thysanozoon* feeds on ooze, and the small algæ and animals on the walls of aquaria.) The same is evidently also the case with the pantopods, which, according to Dohrn (14) are never found with anything in their stomachs. Nemerteans are eaten by fish such as plaice, common dab and long rough dab, cod, and *Onos cimbrius*, *Planaria* on the other hand only now and then by plaice and dab. In *Harmothoë imbricata* and *Neptunea antiqua* I have likewise found remains of Planariæ.

B. Animals with hard prehensile and masticatory organs.

I. Those feeding by means of a radula.

Molusca glossophora:

Turritella terebra L.	(15	specimens	examined	from 5 diff. localities).
Aporrhais pes pelecani L	(17	»	»	» 3 » »).
Chætoderma nitidulum Loven.	(2	»	»	).
Chiton sp.	(9	»	»	from 6 diff. localities).
Tectura virginea Müll.	(1	»	»	).
» *testudinalis* Müll.	(1	»	»	).
Trochus cinerarius L.	(3	»	»	from 3 diff. localities).
Rissoa membranacea Adams	(26	»	»	» 13 » »).
» *inconspicua* Alder.	(6	»	»	» 3 » »).
Hydrobia ulvæ Penn.	(13	»	»	» 5 » »).
Neritina fluviatilis L.	(3	»	»	).
Lacuna divaricata Fabr.	(10	»	»	from 5 diff. localities).
Cerithium reticulatum Da Costa.	(5	»	»	).
Littorina obtusata L.	(2	»	»	from 2 diff. localities).
» *tenebrosa* Mtg.	(3	»	»	» 2 » »).
» *rudis* Mat.	(10	»	»	)
» *littorea* L.	(71	»	»	from 25 diff. localities).

Dendronotus arborescens Müll.	(2	specimens	examined).				
Doris sp.	(4	»	»	).			
Æolis sp.	(13	»	»	from 3 diff.	localities).		
Acera bullata Müll.	(62	»	»	» 10	»	»	).
Philine aperta L.	(120	»	»	» 13	»	»	).
Dentalium entalis L.	(10	»	»	» 5	»	»	).
Neptunea antiqua L.	(91	»	»	» 16	»	»	).
Buccinum undatum L.	(190	»	»	» 21	»	»	).
Nassa reticulata L.	(41	»	»	» 8	»	»	).
» *pygmæa* Lam.	(6	»	»	).			
Natica sp.	(1	»	»	).			
» *pallida* Brod et Sav.	(7	»	»	from 2 diff.	localities).		
Bela turricula Mtg.	(4	»	»	» 3	»	»	).

The three first named species are true detritus eaters, feeding directly on the upper layer of the bottom detritus. The next nine genera live mainly by licking off with the aid of the radula the covering of detritus, small plants, etc. always found on shells, stones, algæ and the like. They must therefore be regarded as herbivorous detritus eaters. The detritus consists mostly of vegetable remains: I have, however, occasionally, as for instance in *Trochus cinerarius* and *Hydrobia ulvæ*, found pure bottom detritus. The larger forms, *Trochus cinerarius*, *Lacuna divaricata*, and *Littorina littorea*, can, however, also bite off the tips of fairly large fresh algæ: the last-named form also devours animal food, such as small bivalves, gastropods, ostracods etc. Ainsworth Davis and Fleure (12) give an excellent description of *Patella's* manner of feeding, which agrees entirely with my own observations of the forms here referred to. Orton however (48) is of opinion that *Crepidula fornicata* and a number of closely related forms are pure detritus eaters, feeding in almost the same way as bivalves, filtering out the suspended detritus from the water by means of the movement occasioned by the cilia of the gills. This is doubtless entirely erroneous; at any rate, I know of nothing corresponding thereto among the Danish gastropod forms. Orton has, moreover, found that the gills of *Buccinum* and *Nassa* are ciliated in the same way as those of *Crepidula*, and from this he ventures to suggest, l. c. p. 473, that detritus must also be of some importance as food for these large gastropods. This is certainly wrong; the stomachs of the animals in question never contain so much detritus as to warrant the presumption of its being of the slightest importance to them as food. Rauschenplat (55) distinguishes incorrectly between *Rissoa octona* and *Cerithium reticulatum* as »Kleinpflanzenfresser« and *Littorina littorea* (»Grosspflanzenfresser«). All the young and small *L. littorea* are, as a matter of fact »Kleinpflanzenfresser«, the large both »Klein«- and »Grosspflanzenfresser«, besides being carnivorous.

In the nudibranchs *Dendronotus*, *Doris* and *Æolis* I have found remains of *Bryozoa* and plant detritus; according to several writers (Meyer and Møbius (41), Marshall, Keller and Hecht) the *Æolidæ* devour living actinians in aquaria, besides *Hydroidæ* and the eggs of other animals (e. g. *Gobius*). There is no doubt

that they feed largely upon *Coelenterata*; it has been shown (e. g. L. Cuénot, in Arch. zool. expér. et gén. IV. Série, Tome VI) that the nematocysts in their dorsal papillæ originate from *Coelenterata* which they have devoured. These animals are therefore carnivorous detritus eaters. The same applies to *Philine aperta* which in addition to bottom detritus also devours the young of *Venus, Astarte, Hydrobia* and small crustaceans (ostracods and bottom copepods), Foraminifera etc. I have found a similar diet in the case of *Dentalium entalis*. *Acera bullata* can, in addition to detritus and animal food, also live on fresh plants; it is therefore a herbivorous and carnivorous detritus eater. Purely carnivorous are the last five genera: *Neptunea, Buccinum, Nassa, Natica* and *Bela*. As shown by the analysis of the contents of stomach, these animals are frequently found with quite empty stomachs, this being the case with no less than 153 of the 190 *Buccinum undatum* examined. One may, however, be fortunate enough to find specimens which have recently swallowed their prey, and exhibiting for instance, a whole worm, soft parts of molluscs, etc. In *Neptunea antiqua, Buccinum undatum, Nassa reticulata, N. pygmæa* and *Natica*, I have thus found muscles, liver cells, and siphons of bivalves (*Macoma baltica, Abra alba,* and others). In addition, I have in *Neptunea* and *Buccinum* found *Polychæta*, such as *Lumbrinereis fragilis, Nephthys sp., Artacama proboscidea, Pectinaria belgica,* etc., besides young specimens of *Echinus* and *Echinocyamus*, a whole *Planaria*, remains of nemerteans(?), and ascidians. In the *Nassa*-species I have found crustaceans, such as *Mysidæ* and *Gammaridæ*. Dr. Petersen (49, p. 38) has, in an aquarium, seen a *Neptunea antiqua* open a *Mytilus edulis* as long as its own shell, and then devour the soft parts. How the large whelks manage to open bivalves has not been definitely explained; probably some secretion from the whelk serves to soften the shell, so that it can then be filed through by the radula (*vide* Lang (29), Fürth (21), Collins (8), Dakin (10) and others). Walther's (64) distinction between herbivorous and carnivorous gastropods based upon the shape of the shells is untenable.

The small gastropods of the plant region are eaten by fish such as plaice, dab, flounder, *Gobius niger* and *Ctenolabrus rupestris, Nerophis ophidion, Zoarces viviparus* and eels; even the large *Littorina littorea* I have once found in the stomach of an eel. The soft parts of *Buccinum* and *Neptunea* are eaten in great quantities by cod: from aquarium observations it would seem that they get rid of the shells by biting into the foot when extended, and then shaking the creature out of its house. In eels, dabs and *Zoarces viviparus* also I have found soft parts of *Buccinum*. Otherwise, the worst enemies of the gastropods are the Echinoderms *Ophioglypha, Echinus, Astropecten Müllerі* and *Asterias rubens, Carcinus mænas, Stenorhynchus rostratus;* and the *Crangon* and *Palæmon* species will, like the *Polynoïdæ*, eagerly devour especially the small *Rissoa, Hydrobia* and *Lacuna* species.

II. Animals feeding by means of a muscular gullet furnished with hard mandibles or teeth.

1. *Polychæta.*

Aphroditidæ: *Aphrodite aculeata* L. (50 specimens examined from 10 diff. localities).
Polynoïdæ: *Lepidonotus squamatus*(L)(64 » » » 16 » »).

Polynoïdæ:	*Harmothoë imbricata* (L)	(17	specimens	examined	from	5	diff.	localities).
	» *sp.*	(1	»	»	).			
	Enipo Kinbergi Mgrn.	(2	»	»	).			
	Gattyana cirrosa (Pall.) Mc. Intosh	(1	»	»	).			
Acoëtidæ:	*Panthalis Ørstedi* Kinb.	(1	»	»	).			
Lumbrinereidæ:	*Lumbrinereis fragilis* Müll.	(19	»	»	from	12	diff.	localities).
Glyceridæ:	*Glycera alba* Rathke	(23	»	»	»	10	»	»).
	» *Goësi* Mgrn.							
Goniadidæ:	*Goniada maculata* Ørsted	(9	»	»	»	6	»	»).
Nephtydæ:	*Nephthys sp.*	(112	»	»	»	27	»	»).
Lycoridæ:	*Nereis virens* Sars.	(2	»	»).				
	» *pelagica* L.	(39	»	»	from	19	diff.	localities).
	» *diversicolor*. Müll.	(11	»	»	»	4	»	»).

All the above forms, with the exception of the *Nereis* species, are purely carnivorous, attacking and devouring their prey alive by means of the muscular, extroversible gullet, which is provided with several pointed teeth or mandibles. As shown by the analyses of contents of stomach and intestines, the chief food of *Aphrodite aculeata* is other worms, especially *Sabiellidæ* and *Terebellidæ*, besides nemerteans; 35 out of 50 specimens examined were found with empty stomachs. The *Polynoïdæ* live on 1) smaller crustaceans such as *Gammaridæ, Cumacea* etc., 2) Echinoderms: small *Ophioglypha* and *Phyllophorus pellucidus,* 3) worms such as other *Polynoïdæ* and *Trophonia,* 4) gastropods as *Philine aperta,* 5) sponges, and 6) *Hydroidæ.* In the aquaria, the *Polynoïdæ* remain as a rule hidden among stones and algæ, when their colours frequently harmonise perfectly with their surroundings. In *Panthalis Ørstedi, Goniada maculata* and *Glycera* species I have not, despite carefully executed examinations, found anything at all, and am therefore of opinion, having in mind also the arrangement of their feeding organs, that they may be regarded as true carnivores. In the case of the *Glycera* species, this is confirmed by Schmarda and Ehlers. In *Lumbrinereis fragilis* I have found *Amphiura*, tube worms, *Trophonia* and nemerteans, small crustaceans, *Hydroidæ* and small bivalves. — 79 of the 112 *Nephthys sp.* examined had nothing in the stomach or intestines; in the remainder I found 1) small bivalves: *Abra alba, Macoma calcarea,* small *Modiolaria* etc., all with crushed shells, 2) worms, *Sabellidæ, Maldanidæ* and small *Nephthys,* 3) crustaceans, *Gammaridæ, Diastylis, Mysis mixta.* — *Nereis diversicolor* is a herbivorous detritus eater, devouring pure bottom detritus and sometimes fresh algæ. *N. pelagica* is in addition carnivorous; I have found *Rissoa, Montacuta, Mysidæ* and *Diastylis,* but more especially sponges, *Hydroidæ* and Bryozoa in the stomach and intestines. Rauschenplat (55) has in *N. diversicolor* also found some small remains of bivalves; this form is therefore possibly also carnivorous at times. In the large form *Nereis virens*, which has the most powerfully developed mandibles, I have found only animal food, viz. the ends of siphons of *Mya truncata.* The *Polychæta* here mentioned, and

in particular *Nephthys*, are sought for by practically all our fishes; it is rarely that one finds a plaice in the Kattegat or the Belt Sea without some remains of *Nephthys* in its stomach. They are also eaten by *Carcinus mænas, Paguridæ*, *Neptunea* and *Buccinum*, as well as *Asterias rubens* and Actinians.

2. *Priapulidæ.*

Priapulus caudatus Lam. (4 specimens examined from 3 diff. localities).
Halicryptus spinulosus v. Sieb. (10 » » » 4 » »).

These must be regarded as carnivorous detritus eaters. In *Halicryptus* I have found remains of polychæte worms, as *Nephthys* and *Spionidæ*. Rauschenplat (55) has in *Priapulus* also found remains of worms, besides sponge needles and quantities of bottom detritus. Apel (1) and Willemoes-Suhm (66) have observed these forms in aquaria. *Priapulus caudatus* I have found in the stomach of plaice, dab, cod, eel, *Zoarces viviparus* and *Gobius niger.*

III. Animals feeding by means of setæ-covered limbs with chitinous cuticle, frequently also having a strong masticatory stomach furnished with chitinous plates.

1. *Crustacea.*

Cirripedia:
- *Balanus crenatus* Brug. (2 specimens examined from 2 diff. localities).
- » *improvisus* Darw. (49 » » » 7 » »).
- » *porcatus* da Costa

Cumacea:
- *Diastylis Rathkei* Krøyer (10 » » » 6 » »).
- *Eudorella sp.* (2 » »).

Amphipoda:
- *Proto ventricosa* O. F. Müller (6 » » from 2 diff. localities).
- *Gammarus locusta* L.
- *Amphithoë rubricata* (Mont.)
- *Ischyrocerus megacheir* (Boeck)
- *Gammaropsis melanops* G. O. Sars (119 » » » 31 » »).
- *Ampelisca macrocephala* Lillj.
- » *Eschrichtii* Krøyer
- *Corophium grossipes* Linn. (3 » » » 2 » »).
- *Moera Lovenii* Bruz. (7 » » » 3 » »).
- *Haploops tubicola* Lilljeborg (14 » » » 4 » »).

Isopoda:
- *Iæra marina* Fabr. (3 » »).
- *Idothea balthica* Pallas (80 » » from 24 diff. localities).

Schizopoda:	*Mysis mixta* Lilljeborg	(41 specimens examined from 6 diff. localities).
	» *spiritus* Norm.	(20 » » » 2 » »).
	» *inermis* Rathke	(26 » » » 9 » »).
	» *flexuosa* O.F.Müller	(41 » » » 8 » »).
	» *neglecta* G. O. Sars	(3 » »).
	Gastrosaccus spinifer Goës	(10 » » from 3 diff. localities).
Decapoda:	*Crangon vulgaris* Fabr.	(93 » « » 14 » »).
	» *Allmani* Kinahan	(18 » » » 7 » »).
	Pandalus Montagui Leach	(10 » » » 5 » »).
	Palæmon Fabricii Rathke	(97 » » » 13 » »).
	» *squilla* Latr.	(12 » » » 5 » »).
	Eupagurus Bernhardus L.	(106 » » » 24 » »).
	» *cuanensis* Thompson	(1 » »).
	» *pubescens* Krøyer	(1 » »).
	Carcinus mænas Penn.	(124 » » from 32 diff. localities).
	Portunus depurator L.	(3 » » » 2 » »).
	Hyas araneus L.	(7 » » » 5 » »).
	» *coarctatus* Leach.	(24 » » » » » »).
	Stenorhynchus rostratus L.	(34 » » » 3 » »).
	Inachus dorsettensis Penn.	(3 » »).
	Homarus vulgaris M. Edw.	(1 » »).
	Calocaris Macandreæ Bell.	(3 » »).

The *Cirripedia* and *Cumacea* examined are pure detritus eaters; the *Balani* live on finely sorted, floating detritus, the *Cumacea* on finely sorted bottom detritus. Rauschenplat (55) calls the *Balani* »Plankton eaters«, but has in reality found far more »undeterminable substances«: remains of plants and bottom diatoms, than plankton in them. The amphipods feed on plant, detritus or animal food or exclusively on detritus according as they inhabit 1) the plant-belt or 2) the unvegetated bottom. To the first named category belong the first 5 amphipod species named in the list above. The detritus food consists mainly of plant detritus and the animal food of crustaceans such as copepods and *Mysidæ*, lamellibranch larvæ etc. The large forms, as for instance *Gammarus locusta,* live mainly on fresh plants and animal food, the smaller ones, and all the young, on plant detritus. To the last category belong the amphipods mentioned in the list above; many of these, such as *Ampelisca* and *Haploops* form tubes of bottom detritus. These tubes stand perpendicularly up from the bottom, about 1000 or more per 1 m^2 of surface. Only in *Moera Lovenii* have I found any animal remains, such as crustaceans, sponges and Bryozoa; otherwise, they are all pure detritus eaters, as a rule sorting out the bottom detritus more or less finely before devouring it. *Idothea baltica, Iæra marina* and the *Mysidæ* from the plant region are herbivorous and carnivorous detritus eaters. Their detritus food is mainly plant detritus, the animal food being, as regards the isopods, mainly other crustaceans such as the young of *Gammaridæ* and *Mysidæ;* the *Mysidæ* themselves

feed on smaller animals such as bottom copepods and ostracods, and mollusc larvae. In aquaria, *Idothea* will even attack young and growing fish. The young of isopods and Mysidæ live, like those of the amphipods, almost exclusively on fine detritus. I have seen *Mysis inermis* in an aquarium feed partly on plant detritus which it draws into the mouth by the fine setae with which it is furnished, partly preying on copepods. *Mysis mixta* and *Gastrosaccus spinifer*, which live on unvegetated bottom, feed on bottom detritus and animal food, the latter consisting mainly of copepods and small amphipods.

As regards the decapods, *Crangon vulgaris, Palæmon Fabricii* and *P. squilla* live on 1) animal food, viz: the small gastropods and bivalves of the plant region (*Hydrobia, Rissoa, Littorina tenebrosa*, the young of *Mytilus* and small *Cardium*), polychæte worms, such as *Polynoïdæ, Nephthys* and *Nereis*, with crustaceans such as copepods, ostracods, *Diastylis, Gammaridæ* and *Mysidæ, Bryozoa*, insect larvæ and young fish. 2) Plant detritus; this applies especially to the younger specimens. 3) fresh plants, especially the tips of algæ. Rauschenplat (55) calls *Crangon vulgaris* and *Palæmon squilla* mainly carnivorous; these live, however, doubtless as much on detritus and plants. In conformity with this, Ehrenbaum (17) points out that *Crangon vulgaris* at times will feed on the ooze of the bottom, and I have myself seen in an aquarium a *Palæmon squilla* live for a whole year almost exclusively on detritus. *Crangon Allmani* and *Pandalus Montagui*, on the soft bottom outside the plant belt, live on 1) Crustaceans (*Gammaridæ, Mysidæ, Cumacea*), 2) Polychæte worms (*Polynoïdæ, Nephthys* etc.) besides 3) bottom detritus. They are thus carnivorous detritus eaters. This also applies to the hermit crabs: *Eupagurus Bernhardus* feeds on 1) small bivalves (*Mytilus, Cardium, Modiolaria, Abra* (?), *Corbula* and *Nucula*), 2) crustaceans (Ostracods, Mysidæ, *Diastylis, Gammaridæ*, (apparently they devour the tubes in which *Haploops* lives, together with the animal itself) and 4) Echinoderms (*Ophioglypha albida, O. texturata, Echinocyamus pusillus*) and even perhaps fish: an otolith of a small gadoid found in the stomach would seem to suggest this. At the same time, however, the stomach also contains so great a quantity of bottom detritus (as a rule with a quantity of decomposing *Zostera* particles) that this must indubitably form an essential part of the animal's food. In conformity with this, Jackson (27) has seen *Eupagurus* carrying sand to its mouth with its chelae. *Carcinus mænas*, on the other hand, is almost exclusively carnivorous. In the *Zostera* region it lives mainly on gastropods, such as *Rissoa, Hydrobia, Littorina* (often large specimens, the shells being removed by means of the claws) and bivalves such as *Mytilus* and *Modiolaria*, besides crustaceans such as *Gammaridæ, Mysidæ* and *Crangon*, but also small fish such as the *Gobius, Gasterosteus*, and *Syngnathus* species. On rare occasions, also, I have found vegetable remains (green and brown algæ) in the masticatory stomach; they can thus also be herbivorous. I have seen a crab in an aquarium capture 17 *Gobius Ruthensparri* in four days with the aid of its claws, and eat them; in the same time it also ate a quantity of *Rissoa membranacea*. Outside the *Zostera* region, the *Carcinus mænas* lives on bivalves such as *Macoma baltica, Abra, Nucula nitida, Cardium* and *Mytilus;* the shells are crushed by means of the claws and mandibles. Of the polychæte worms this animal is especially fond of *Pectinaria Koreni:* I once found no less than 15

recently devoured *Pectinaria* in the stomach of a crab. I have also found remains of *Harmothoë imbricata* and *Styela,* and carrion is frequently eaten, as may be observed in harbours and fish traps. In *Portunus depurator, Hyas coarctatus* and *Inachus dorsettensis* I have only found animal food, viz: *Ophioglypha albida, O. affinis, Cardium minium, C. fasciatum,* and smaller crustaceans such as *Gammaridæ.* In *Hyas araneus* and *Stenorhynchus rostratus* on the other hand, I have found both vegetable and animal food, viz: in addition to *Ophioglypha albida, Asterias rubens, Echinocyamus pusillus,* bivalves, small gastropods, worms, small crustaceans, ascidians and Bryozoa, also algæ.

Homarus vulgaris is also evidently both carnivorous and herbivorous; I have in one young specimen found remains of mollusc shells and algæ; this agrees with the statements of Herrick (25) who also states that the indigestible parts are ejected again by way of the mouth. This is doubtless also the case with several other crustaceans; I have for instance often compared the contents of the intestines with that of the stomach, and found that *Palæmon Fabricii,* for instance, frequently has the latter full of gastropod shells, skeletons of crustaceans etc. whereas the intestines at the time contained nothing but a fine mass entirely free from skeletal parts.

Calocaris Macandreæ is apparently a carnivorous detritus eater, like the *Paguridæ.* I have found its intestines to contain, besides bottom detritus, also remains of *Goniada maculata.*

When changing their shells, the decapods are always found with empty stomach. In the spawning period also, crustaceans often appear to be fasting, a feature which I have found common to a number of different animal forms.

The enormous swarms of *Mysidæ, Gammaridæ* and isopods in and without the plant belt are eaten by practically all kinds of fish and other carnivorous animals; the *Crangon-* and *Palæmon* species, as well as the *Cumacea,* are also a favourite food of fish, the last-named being also eaten by carnivorous worms and Echinoderms. The *Balani* for instance, are eaten by *Echinus esculentus.* The larger crustaceans such as *Carcinus mænas, Portunus depurator,* the *Eupagurus* and *Hyas* species on the other hand, are eaten by fish, especially cod and sharp-nosed skate. *Stenorhynchus rostratus* and *Inachus dorsettensis* I have found in cod and sea-scorpion; *Calocaris Macandreæ* in *Gadus minutus.* Lobsters, however, I have never found in the stomach of any fish, though according to Summer, Osburn and Cole (61) they are said to be eaten for instance by sharks.

2. Diptera larvæ. (7 specimens examined from 4 diff. localities).

The Diptera larvæ examined belong to various genera of gnat, including the genus *Chironomus.* All live on plant or bottom detritus, and are thus true detritus eaters. They are eaten by fish such as eel and viviparous blenny, stickleback, *Spinachia* and *Gobius,* also by *Palæmon squilla* and *Asterias rubens.*

IV. Animals feeding by means of a masticatory organ with five calcareous teeth.

Echinoidea gnathostomata:

Echinocyamus pusillus Müll. (47 specimens examined from 8 diff. localities).
Echinus miliaris Forb. (56 » » » 16 » »).

Strongylocentrotus drøbakiensis Müll. (184 specimens examined from 28 diff. localities).
Echinus esculentus L. (5 » » » 2 » »).

In *Echinocyamus pusillus* I have found, besides bottom copepods, small gastropods and Echinoderms *(Ophioglypha?)*, also quantities of bottom detritus; this animal must therefore, as suggested by C. G. Joh. Petersen (52) and Eichelbaum (18) be reckoned as a carnivorous detritus eater. *Echinus miliaris* and *Strongylocentrotus drøbakiensis* are herbivorous and carnivorous detritus eaters; by means of their pointed teeth they gnaw off pieces of fresh plants, and also devour, in addition to bottom detritus (especially dead fragments of *Zostera* from the bottom) the animals found on the plants, especially Bryozoa, sponges and *Hydroidæ*. I have, moreover, in *Strongylocentrotus drøbakiensis* found remains of small gastropods, worms (e. g. *Aphrodite aculeata*), crustaceans (e. g. *Gammaridæ* and small *Balani*), Echinoderms *(Ophioglypha robusta* and *O. albida)*, and ascidians. The shells of various bivalves, found by Eichelbaum (l. c. p. 235) in this animal have doubtless been merely dead shells from the detritus layer of the bottom. In *Echinus esculentus* I have found only animal food, viz: *Balani, Pomatoceros,* gastropods and *Hydroidæ.*

I have found *Echinocyamus pusillus* in the stomach of hermit crabs, *Hyas araneus, Astropecten Mülleri*, plaice and dab. *Str. drøbakiensis* I have found in considerable quantities in the stomach of cod taken in the Sound.

If we glance back for a moment at the results of the food investigations referred to in the foregoing, it is at once evident, that detritus food is of extreme importance to the fauna of the sea bottom (Table 2). In looking through the Danish animal communities one by one, as described by Dr. Petersen (50), it will be seen that practically all the characteristic animals, i. e., the most common and most evenly distributed forms (50, p. 5 *seq*) are pure detritus eaters. This is for instance the case with all the bivalves, the extraordinarily numerous *Spatangidæ*, many worms, crustaceans (e. g. *Haploops tubicola)* and gastropods such as *Aporrhais* and *Turritella.* Next in order of frequency come the herbivorous detritus eaters, among which the small gastropods of the plant region are especially important. The animals mentioned may be called producers in contradistinction to the remainder, the consumers, and we find that the proportion between producers and consumers in all the Danish animal communities invariably shows a distinct superiority of the former (Table 3). There is nothing surprising in the discovery that the purely carnivorous animals are relatively least common in the Danish communities, since they are forced to live by preying on other animals. Among the producers there are some forms which when fully grown are rarely, if ever, eaten by other animals, viz. the large detritus eating *Spatangidæ: Brissopsis, Echinocardium* and *Spatangus.* In addition, a number of large bivalves: *Cyprina islandica, Modiola modiolus, Pecten* and *Mya* species, *Mytilus, Cardium* and oysters, besides gastropods such as *Turri-*

Table 2.[1])

True detritus eaters.	Herbivorous detritus eaters.	Herbivorous and carnivorous detritus-eaters.	Carnivorous detritus-eaters.	Herbivorous and carnivorous.	True carnivores.
(Foraminifera)	*Chiton sp.*	*Littorina littorea*	*Ophiopholis aculeata*	*Carcinus mœnas*	*Asteroidea*
(Porifera)	*Littorina rudis*	*Acera bullata*	*Ophiothrix fragilis*	*Hyas araneus*	*Actiniidæ*
Lamellibranchia	— *tenebrosa*		*Ophioglypha robusta*	*Stenorhynchus*	*(Hydroidæ)*
Ascidiæ	— *obtusata*	*Nereis pelagica*	— *affinis*	*rostratus*	*(Nemertini)*
Amphioxus lanceolatus	*Cerithium reticulatum*		— *albida*	*(Homarus vulgaris)*	*(Planaria)*
Most *Polychæta*	*Hydrobia ulvæ*	Some *Amphipoda*	— *texturata*		*(Pantopoda)*
Holothurioidea	*Rissoa membranacea*	— *Mysidæ*	— *Sarsii*		
(Bryozoa)	— *inconspicua*	*Isopoda*			*Neptunea antiqua*
Sipunculidæ	*Trochus cinerareus*	*Crangon vulgaris*	Nudibranchs		*Buccinum undatum*
Echiurus Pallasii	*Lacuna divaricata*	*Palæmon Fabricii*	*Philine aperta*		*Nassa reticulata*
Balanoglossus Kuppferi	*Tectura virginea*	— *squilla*	*Dentalium entalis*		*Natica sp.*
Echinoidea atelostomata	— *testudinalis*				*Bela turricula*
Amphiura Chiajei		*Echinus miliaris*	*Priapulus caudatus*		
A. filiformis	*Nereis diversicolor*	*Str. drøbakiensis*	*Halicryptus spinulosus*		Some *Polychæta*
			Moera Lovenii		
Turritella terebra			*Mysis mixta*		*Portunus depurator*
Aporrhais pes pelecani			*Gastrosaccus spinifer*		*Hyas coarctatus*
Chætoderma nitidulum			*Crangon Allmani*		*Inachus dorsettensis*
			Pandalus Montagui		
(Ostracoda)			*Eupagurus Bernhardus*		*Echinus esculentus*
(Bottom copepods)			— *cuanensis*		
Cirripedia			— *pubescens*		
Cumacea			*(Calocaris Macandreæ)*		
Some *Amphipoda*			*Echinocyamus pusillus*		
Diptera-Larvæ.					

[1]) The forms noted in parentheses have not been sufficiently investigated to permit of their food being stated with certainty. The systematic groups such as the *Lamellibranchia, Ascidiæ* etc., here indicate only such of the animals belonging to the group in question as have been examined.

Table 3.

Quantity of **Producers** and **Consumers** in the animal communities i

		Bivalves	Gastropods		Worms	
		Producers. (Detritus eaters)	Producers (Herbivorous detritus eaters)	Consumers. (Carnivores and carnivorous and herbivorous detritus eaters)	Producers. (Detritus eaters)	Consumers. (Carnivores and carnivorous herbivores)
Kattegat.	Nr. 1. *B. n.* Stations	15,35	1,07*)	0,55	17,55	6,47
	» 2. *B. T.* Stations	25,34	57,98*)	1,89	9,77	16,27
	» 3. *E. T.* Stations	24,03	103,49*)	3,43	4,53	4,98
	» 4. »*Haploops*« Stations	39,50	—	3,11	26,89	11,57
	» 5. *E. (v.)* Stations	124,61	4,66[1])	1,99	3,70	2,55
	» 6. *E. v.* Stations	40,75	0,59*)	0,86	2,61	3,04
	» 7. *V.* Stations	31,31	0,09	0,25	2,65	3,35
Samsø Belt.	» 8. Rich *E. b. c.* Stations	185,82	1,63[2])	5,56	3,86	16,04
	» 9. Poor *E. a. b. c.* Stations	39,55	0,99[3])	0,18	1,32	7,44
	» 10. *d.* Stations and allied St.	30,94	0,14	2,11[5])	2,43	1,01
Great Belt.	» 11. *a. b c.* Stations, influenced by *R. M.*	516,89	0,54	11,66	13,97	21,40
	» 12. N. of Sprogø. — *a. b. c.* Stations, often with *E.*	58,22	0,22[4])	0,05	3,08	16,91
	» 13. S. of Sprogø. — *a. b. c.* Stations, generally without *E.*	157,79	0,01	2,51	2,28	8,08
	» 14. Poor *a. b. c.* Stations without *E.* and without grown *Cyprina*. — Shallower water	17,29	0,01	1,09	2,52	6,94
	» 15. *d.* Stations, Nyborg Fjord	4913,79	3,56	65,87[6])	4,19	0,58
	» 16. *d.* Stations, N. of Sprogø	33,89	0,09	1,35[7])	0,71	1,91
	» 17. *d.* Stations, S. of Sprogø	342,37	0,15	0,69[8])	1,22	1,04
Little Belt.	» 18. *a. b. c.* Stations, generally with *Cyprina*	140,38	—	28,84	2,37	2,46
	» 19. *d.* Stations	83,70	7,76	12,73[9])	6,44	0,66
Western Baltic.	» 20. *a. b. c.* Stations, often with *Cyprina* and sometimes with *d.*	94,41	—	0,05	3,01	5,73
	» 21. *d.* Stations	68,17	—	—	7,93	1,23
True Baltic.	» 22. *d.* Stations	142,56	—	—	1,83	0,46
	» 23. *d.* Stations, also *a.*	147,17	—	—	1,59	0,31

*) only *Turritella terebra* and *Aporrhais pes pelecani*. — [1]) of this *Turritella terebra* and *Aporrhais pes peleca* [4]) of this *Aporrhais pes pelecani* 0,18 gr. — [5]) of this *Littorina littorea* 0,90 gr. — [6]) of this *Littorina littore* *Littorina littorea*.

nside the Skaw, expressed in **gr.** (rough weight) **pr. m²**.

Echinoderms		Crustaceans		Ascidians	Actinians	Hydroidæ	*Foraminifera*	*Porifera*	*Amphioxus lanceolatus*	Fishes	Total	
Producers. (Detritus eaters)	Consumers. (Herbivorous and carnivorous detritus eaters)	Producers. (Detritus eaters)	Consumers. (Herbivorous and carnivorous "detritus eaters	Producers. (Detritus eaters)	Consumers. (Carnivores)	Consumers. (Carnivores)	Producers. (Detritus eaters)	Producers. (Detritus eaters)	Producers. (Detritus eaters)	Consumers. (Carnivores)	Producers	Consumers
158,29	1,65	0,45	2,10	—	0,16	—	—	—	—	1,41	192,71	12,34
240,02	0,12	0,12	0,50	0,46	2,54	—	0,01	0,14	—	—	333,84	21,32
227,01	4,30	0,07	1,86	0,20	0,02	—	—	—	—	—	359,33	14,59
84,45	9,23	18,40	1,31	—	0,17	—	—	—	—	—	169,24	25,39
159,04	7,27	0,31	0,88	0,48	0,15	—	—	—	0,36	—	293,16	12,84
284,84	1,31	0,43	0,15	—	0,01	—	—	—	0,16	—	329,38	5,37
0,06	6,25	0,01	2,14	—	—	—	—	—	—	—	34,12	11,99
109,91	7,09	0,29	0,03	—	0,13	—	—	—	—	—	301,51	28,85
124,59	12,53	0,70	—	0,01	0,20	—	—	—	—	—	167,16	20,35
—	0,20	0,03	0,08	—	—	—	—	—	—	—	33,54	3,40
129,64	106,53	261,96	—	81,11	0,16	1,34	—	3,82	—	—	1007,93	141,09
49,29	4,24	0,51	0,52	—	0,04	0,17	—	—	—	—	111,32	21,93
0,94	7,48	0,82	0,07	11,53	—	—	—	1,13	—	—	174,50	18,14
—	5,47	0,07	—	—	—	—	—	—	—	—	19,89	13,50
—	2,73	0,01	3,15	0,04	0,04	—	—	—	—	—	4921,59	72,37
0,01	0,33	0,01	5,23	—	—	—	—	—	—	—	34,71	8,82
—	3,38	0,05	0,23	—	0,05	—	—	—	—	—	343,79	5,39
2,25	10,77	0,03	1,04	7,53	—	—	—	—	—	—	152,56	43,11
—	1,53	0,06	0,03	0,20	0,15	—	—	—	—	—	98,16	15,10
—	4,23	0,14	0,03	7,45	—	—	—	—	—	—	105,01	10,04
—	0,60	0,03	0,10	—	—	—	—	—	—	—	76,13	1,93
—	—	0,11	0,10	—	0,01	—	—	—	—	—	144,50	0,57
—	—	0,13	—	3,96	—	—	—	—	—	—	152,85	0,31

ni 4,63 gr. — [2]) only *Aporrhais pes pelecani*. — [3]) of this *Aporrhais pes pelecani* 0,95 gr. —
i 63,93 gr. — [7]) only *Littorina littorea*. — [8]) of this *Littorina littorea* 0,58 gr. — [9]) only

tella, Aporrhais, and large *Littorina littorea,* crustaceans such as lobster and *Balani,* worms as *Arenicola marina* (in the shallowest water), and, finally, Anthozoa such as *Alcyonium digitatum, Pennatula phosphorea* and *Virgularia mirabilis.*

The main result of the present investigations may be briefly summed up as follows:

Detritus forms the principal food of nearly all the invertebrate animals of the sea bottom, next in order of importance being plant food from fresh benthos plants. The value of the live phytoplankton in this connection is absolutely minimal, amounting in any case to nothing more than an indirect significance through the medium of the plankton copepods.

By collecting and measuring the fæces secreted during a certain period, say of 24 hours, either in aquaria, or, in the case of *Arenicola,* in a state of nature, I have obtained the following figures showing the amount of food passed through the alimentary canal in the space of 24 hours. (All figures for dry weight).

1) *Mytilus edulis,* Thisted Bredning $^{1}/_{6}$ 1912	1,87	gr	Detritus	pr. 100 gr	*Mytilus.*
Vejle Fjord, $^{26}/_{6}$ 1912	3,08	-	—	—	—
2) *Modiola modiolus,* W. of Hjelm, 33 m, $^{27}/_{6}$ 1912	2,83	-	—	—	*Modiola.*
3) *Ciona intestinalis,* Isefjord, $^{18}/_{8}$ 1913	0,59	-	—	—	*Ciona.*
4) *Phallusia aspersa,* Limfjord, $^{22}/_{7}$ 1913	1,20	-	—	—	*Phallusia.*
5) *Arenicola marina,* Nyborg Fjord, $^{18}/_{12}$ 1913	6,98	-	—	pr. individual (average).	

All these figures are necessarily only minimal values; even then, however, the quantities resulting in course of time will be very considerable, if we calculate the amount of detritus annually deposited in the form of excrements pr. 1 m² at different places. In Nyborg Fjord, for instance, we have 18500 gr *Mytilus edulis* pr. 1 m² *(vide* (50), Appendix p. 35), which gives 4178 gr. dry detritus annually pr. 1 m². The figures for *Modiola* in Samsø Belt are 1616 gr. and 5196 gr. pr. 1 m², those for *Phallusia* in the Limfjord on the other hand being only 10,63 gr. pr. 1 m² annually. Finally in the case of *Arenicola marina,* we find an annual excretory production of 112128 gr. pr. 1 m² (dry weight). Davison (13) has by similar investigations obtained a figure of 477750 gr. dry matter pr. 1 m² per annum.

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The Work of the Biological Station from 1889—1914.

As far back as 1882—83, Professor *Japetus Steenstrup* invited the then stud. mag., later Dr. phil. *C. G. Joh. Petersen* to take part in some cruises on board the fishery inspection vessel »Hauch« for the purpose of making zoological studies in the Danish waters. The officer in command of the »Hauch« was then Lt., later Commandør *C. F. Drechsel*. These investigations were subsequently continued under the leadership of Professor *Chr. Lütken*, who succeeded *Steenstrup* as professor of zoology. In the first four years, from 1883 to 1886, were made those collections in the Kattegat, upon which was based the later publication: »Det videnskabelige Udbytte af Kanonbaaden Hauch's Togter«, 1893, 4to, Atlas in folio, published by *C. G. Joh. Petersen*. In 1888, Dr. *Petersen* wrote his treatise for the degree of Dr. phil.: «Om de skalbærende Molluskers Udbredningsforhold«, the work being based on some of these investigations.

Dr. Petersen continued also after 1886 to prosecute his investigations. under other commanders of the gunboat, at government expense; now, however, paying especial attention to fishery-biology, a subject in which he had gradually become interested through intercourse with the fishermen and observation of the fishery. The government desired such investigations to be undertaken, in continuation of the earlier work of *H. Krøyer, Chr. Lütken, G. Winther* etc., which had been interrupted by *Winther's* premature decease.

In the earliest fishery reports for the years 1888 and 1889, we find the first biological investigations made by *Dr. Petersen* with regard to the life of the plaice, and carried out partly by means of the »Marking Method« discovered by himself, a method which was immediately adopted and found successful in the Kattegat. The study of the biology of fish from the egg to the oldest stages was also then commenced.

Biological investigations in the true sense, however, could not long be carried out exclusively from the inspection vessel, which had many other duties to attend to. In 1899 therefore, by the initiative and co-operation of Captain *C. F. Drechsel*, then Fishery Consulent, and Professor *Lütken*, a so-called *Biolo-*

gical Station was started. The station consisted of an old transport vessel formerly belonging to the navy, and now transformed into a laboratory, intended to lie at anchor in such small waters as were to be further investigated. A small open motor boat and an open sailing dinghy were also attached to the Station. *Dr. Petersen* was placed in charge of the Station on the 1st August 1889, and has since, as Director, continued the work in question up to the present date.

The necessary alteration of the vessel was carried out during the winter of 1889—90 by shipbuilder *Lind-Hansen*, in Odense. Since that time, the Station's anchorages have been as follows:

1890. Holbæk Fjord. Winter in harbour at Copenhagen.
1891—92. Fænø Sound, off Esbenhoved, with winter quarters at Kolding.
1892. Svendborg Sound, off Troense. Winter at Thurø.
1893. Kerteminde. In this year, the Station obtained a small decked sailing boat of about 5 tons, »Makrelen«, to assist in the investigations.
1893. In the autumn to Stege, spending the winter there.
1894. In the spring to Frederikssund, wintering there.
1895—96. Nykøbing, in the Limfjord.
1897. To Frederikshavn.
1898. On the 14th September, to Nyborg. In 1899, the Station obtained the loan, and later possession, of a small steamer, the »Sallingsund«, formerly in in the service of the State Railways. Since that time, the Station has had its permanent quarters at Nyborg, save for a short time in the spring of 1902, when it was anchored in Fænø Sound for the purpose of special studies. From this time onward, the investigations have been chiefly made from the steamer, the Principal and Assistant having therefore their quarters on board, as a rule for about 7 months of the year. Neither the steamer nor the transport are suited to winter work, and it is thus only rarely that investigations have been carried out for any considerable time at this season.

Various younger men have acted as Assistants at the Station, among whom may be mentioned:

Engineer *P. Gudme,* cand. mag. *E. Kofoed,* cand. mag. *Hørring,* cand. mag. *Andr. Otterstrøm,* cand. mag. *Chr. Løfting,* cand. mag. *Chr. Lunn,* cand. mag. *Gemzøe,* Dr. phil. *Johs. Schmidt,* Dr. phil. *Th. Mortensen,* Dr. phil. *H. Ostenfeld.* Many of these scientists have since gone over to various branches of fishery work. It is only of late years that the salary of the Assistant has been brought up to a figure which can be regarded as fairly adequate; cand. mag. *H. Blegvad* has now been acting as Assistant for some years, and Dr. phil. *Boysen Jensen* has assisted the Station with plant-physiological investigations.

Numerous foreign scientists have stayed for short periods at the Station in order to make themselves acquainted with the methods of investigation; the small steamer has not sufficient accomodation for visitors for extended periods of work. Such visits have been made, not only by scientists from the northern countries of Europe, but also from the Mediterranean, America, and India, and have naturally served to render the work and its results widely known.

Among the fishermen who have been attached to the Station, none have

been of greater service in its developement than *Johannes Johansen (Høj)* from Kerteminde; his sons, *Carl Johansen* and *Niels Johansen* have assisted him in the work. *N. Johansen* is now captain of the »Sallingsund«.

The Station has published XXI Reports of investigations during these 25 years, all of which have been printed in the »Fiskeri-Beretning« and written for the most part by Dr. *Petersen*. Among other writers who have furnished contributions the following should be mentioned:

Dr. *Th. Mortensen*, Dr. *Kolderup-Rosenvinge*, cand. mag. *Chr. Løfting*, cand. mag. *Gemzøe*, cand. mag. *Andreas Otterstrøm*, the Norwegian Professor *H. H. Gran*, Dr. phil. *H. Ostenfeld*, and Dr. phil. *P. Boysen Jensen;* a series of names representing both zoology and botany. The most important papers are mentioned in the summary p. 86—88; in addition, reference may be made to *Sven Dahl's* Biblioteca Zoologica Danica, 1876—1906 (1910). It should be noted that the work of the Station has been extended to many different regions within the sphere of scientific-practical marine biology, and has not been restricted to scientific specialism, keeping closely to the lines laid down in the Station's scheme of work, viz: »that the object of the Biological Station is to procure information concerning all such questions within the range of natural science as may be of importance for the furtherance of practical fishery and serve to elucidate problems connected with legislation for the fishery.«

Methods of work and investigation invented by the Station.

Among the methods discovered and developed by the Station may be mentioned:

1) The marking of fish in the sea for scientific purposes, in order to study their growth and migrations, and in addition, to obtain some idea as to the intensity of the fishing (i. e. its effect upon the stock).

2) Determination of the age and growth of the fish by measurement of great numbers of individuals (Report I); this method has since been improved and supplemented by investigation of the growth rings in the scales and bones.

3) Augmentation of the stock of fish in smaller waters by restocking with young plaice from the overpopulated areas of the sea.

4) Capture of eels by directing the movements of the fish with strong light. These experiments were suspended, as far as the Station was concerned, on account of the uneasiness occasioned among the fishing population, who feared lest too many eels should be taken at one place.

5) Quantitative investigation of the bottom fauna (Valuations) both by means of the bottom sampler and by diving work. One such investigation by means of divers led to the discovery of the great stock of oysters, and consequent increase of the rental charge.

6) Various new apparatus for investigation purposes have been constructed and employed; in addition to the previously mentioned bottom samplers for quantitative work, may be mentioned an otter seine for use in deep water (Report VIII. 1898), by means of which the large Norwegian prawns,

for instance, were found in quantities in the Christiania Fjord in 1897 with assistance of Dr. *Johan Hjort*, and later also in the Gullmarfjord, in Sweden. This net has since done good service in numerous other investigations, and is still used, albeit in a somewhat altered form, at the Station.

The so-called Petersen's young-fish trawl, for the capture of young fry in the intermediate water layers has also been, and is still increasingly used.

7) Experiments with preparations for increasing the life of nets have been carried on for many years, and a new material, »Virit« which is still on sale, was discovered with the aid of Professor *E. Kofoed;* with regard to this important question, however, further developements doubtless remain to be made.

Some results attained by the work of the Station.

Prior to the institution of the station it was generally supposed that many of our food-fishes had their spawning grounds in the small fjords and creeks along our coasts, and to this supposition was doubtless due, at least in part, the regulation concerning »closed waters« in the Fisheries Act of 1888. Its effect was further marked by the equipment of the Station itself with apparatus which could only be used for investigation of such minor waters. It was soon found, however, that food-fishes such as the cod and allied species, the flat fish, and the eel, had their spawning grounds elsewhere. With the assistance of various inspection vessels and guard ships, this was shown to be the case, and the idea of improving the fishery mainly by augmenting the number of fish, through artificial hatching in the sea, as in Norway and America, was soon, thanks to the investigations, replaced by the theory that an increase in the size of the fish would be of more effect, especially in the case of the flat fish, (Theory of growth v. Theory of propagation. *Vide* Report IV, 1894: On the Biology of our Flat-fishes and on the decrease of our Flat-fish fisheries) and that attention should rather be directed towards protective measures in the form of size-limits for such fish. The Report IV above referred to, in which these questions are discussed for the first time, and where statistics, the marking system, and determinations of age by means of measurement are included in the investigations, forms the first foundation for studies of this nature, and is also, supplemented by recent methods, employed as such to the present day.

The hatching of marine fish has hitherto not been greatly esteemed, at any rate in Europe; possibly the stock of fish may so decline as to render the employment of the method, with adequate technical improvements, an advisable step. Up to the present, however, this has not been the case.

With regard to legislation, these altered points of view have been of great importance; if the »closed water« system is to be pursued, it must now be done on other grounds, and many of the restrictions in question have been abolished by the act of 1907, the first instance of general fishery legislation in which the results of the Station's work have been of any effect. Improved size limits have been introduced in that year for various species of fish, partly on the basis of biological investigations carried out; these need not however, here be treated in detail.

With regard to the great anxiety as to the detrimental effect of the bottom seine on the food of the fishes of the bottom, the Station has never been able to find any justification of this fear, and the method in question is now generally employed throughout our waters, nor has any instance been furnished of destruction occasioned thereby.

A point of extreme importance to the legislation concerning eel fishery was the Station's demonstration of the fact, already mooted as a theory by some, that the eels on attaining maturity, assume a special spawning dress, and become silver eels; these silver eels, having once left our waters, never return, and should therefore be captured without restriction on their outward way. This proof, brought forward in Report V, 1896, together with information as to the great difference in size between grown up male and female eels in our various waters, was the first principle for determination of the correct size limit for this species of fish. Since then, investigations in the Atlantic have largely contributed to the furtherance of the question as to the true spawning grounds of the eel; that the species does not spawn in Danish waters has long been known.

In a country such as Denmark, where the fishing industry is carried on to such a degree of intensity, it is not to be expected that important new fisheries should often be discovered; the Station has, however, beyond all anticipation, succeeded in effecting something in this direction, in the year 1899—1900, when experiments with new apparatus were being made on board the »Sallingsund« with a view to discovering the most suitable form of implements for investigating the stock of fish. These experiments were commenced in the Great Belt, close to the Station, and it was soon noted that a surprisingly large amount of plaice were taken in the small seine nets, while the fishermen working the Belt were complaining of the poor quantities of plaice caught by their gill nets; seine nets for plaice being then practically unknown in those localities. The big hauls made by the Station, especially south of Sprogø, gradually became noised abroad, and the news, briefly mentioned in a local paper (Nyborg Avis), reached among other places Frederikshavn, whereupon some large cutters immediately appeared on the scene with »Snurrevaad«, and made good catches. In course of time, a great number of plaice cutters, of a size suitable for work in the Belt Sea, appeared from Fünen and Zealand, and the seine fishery, as carried on among the famous plaice of the Kattegat, was soon at work among the poorer fish of the Belt Sea. The statistics for the plaice fishery in the Belt Sea show a steady advance, from about 100,000 Kr. annually before 1899 to over 500,000 Kr. in 1911, rising then to over 1 million Kr. in 1912; a figure for this last named year almost equal to the value of the plaice fishery in the Kattegat, the Belt fishery, moreover, considerably exceeding that of the Kattegat in point of actual weight of fish caught. The motor industry is of course responsible for the rapid developement of these small fishing boats, of a tonnage suitable for our waters; for seine fishery especially the motor boat is excellently adapted.

It is impossible to set forth all the results which the investigations made by the Station have procured throughout the fishing industry; one astonishing fact however, is that the fishermen themselves are often found to be acquainted

with these investigations, their knowledge being doubtless due, not so much to the printed Reports as to the constant communication by word of mouth which naturally results from the continual presence of the »Sallingsund« and its crew among the fishing population. It is not always possible to say whence they have their knowledge, the main point, however, is that it is there. The spread of information thus occasioned, supported as it has been of late by the work of the Fishery High School, is of no little value.

The two methods above referred to, viz: the restocking of the Limfjord with plaice, and the new method of working the oyster fisheries, bring in each year, partly in profits for the fishermen, and partly in direct payments to the State, sums so considerable that the expenditure towards the upkeep of the Station becomes inconsiderable in comparison therewith; in a word, the Station is actually a paying concern.

It is difficult to furnish exact figures for the profit accruing to the Limfjord fisheries from the restocking; since 1908, however, when the work began, the yield of flat-fish in the Limfjord has as a rule been from 1—200,000 Kr. in excess of the average figures for the years before that date, despite the fact that restocking work had been previously carried on, though to a lesser extent. Of late years, about 2 million young plaice have been annually transplanted to this water, at a cost of some 20,000 Kr.

The Oyster Fisheries yielded, in the decade from 1900—1909, an average annual revenue of 70.000 Kr. to the State. Since the introduction of the new rental tariff, they have furnished 145,000 Kr. in rental alone, and will in the future give still more according to the new and amended conditions, which include, moreover, plans for improvement of the fishery by the application of new methods of working.

It would therefore seem but reasonable, that the Station should soon be granted the means of fulfilling a long-felt want; i. e., the erection of fixed premises on land, with aquaria for investigations which it has hitherto been impossible to deal with, the Station at the same time being promoted to a permanent institution, to which young men can devote their services with the prospect of regular employment. If the work of the station is to be maintained in accordance with its traditions, this should be done at an early date. Dr. *Petersen*, who has throughout been the Director of the Station, has hitherto upheld these traditions singlehanded, having for the part 25 years devoted himself exclusively to the work of the station, save only for such other tasks as have devolved upon him by order of the Ministry itself. He is now 53 years of age. —

The work in connection with fresh-water fishery has in the main, consisted of 1) the development of methods of capture so as to ensure the taking of the greatest possible number of fish. This led to the discovery that certain species require, 2) protective measures, which have accordingly been introduced; in both of these phases our salt water fisheries have followed the same lines. Both branches of fishery have finally endeavoured by means of 3) incubation, regulation of numbers, and transplantation of small fry, etc. to promote the developement of the stock.

A further step in this direction has been the campaign aginst 4) the

enemies of the food-fish, such as otters, birds, etc.; here also, the work has embraced both fresh and salt water (seals etc.). Great endeavours have been made to procure for the fresh water food fish, 5) increased nourishment, partly by extermination of less valuable species which diminish the common food supply, and partly by improving the conditions which determine the developement of the fauna whence such nourishment is derived (by appropriate treatment of the bottom). This has, however, only to a slight degree been carried out in salt water, save for the clearing of oyster beds, etc., primarily, of course, owing to the fact that the fresh waters are as a rule of more limited extent, and therefore easier to deal with, also experimentally; ponds and small lakes for instance, may easily be dried out etc. There are, it is true, many salt waters e. g. in Denmark, which might, as regards their size, be similarly dealt with, and their subjection to such methods is doubtless only a question of time; we know, however, far less as to how such methods should be applied in salt water, and it is with a view to the elucidation of such problems that the valuation experiments carried out of late years from the Station were instituted. How far these may succed, the future must decide; should the object in view be attained, this would give us approximately the same methods of procedure for both salt and fresh water. — This much may be said as to the productivity of the sea, that it is only in the vicinity of the coasts, and in shallower, more sheltered waters, that the greatest numbers of fish, and therefore also the greatest numbers of food fish, per hectare of bottom are found. Only here, therefore, can an extensive production in proportion to the area concerned be expected, and to such waters the great and remunerative fisheries must consequently be restricted. The bottom of the great oceans must in particular be mainly regarded as desert. In view of the fact, however, that our salt water fisheries for bottom fish yield on an average only 10—20 kg. fish per hectare per annum, whereas certain fresh-water lakes in Germany and elsewhere yield, under rational methods, 50—100 kg, and carp ponds many times that quantity, it will be seen that we are yet far from having arrived at the right methods.

Moreover, when we consider that edible mussels, (e. g. »Pælemuslinger«) are to be found at certain places in our fjords to the extent of many thousand kg. per hectare, it would seem possible that with proper treatment, a far greater yield should be obtainable in such areas than is furnished by fish. Fish are for the most part carnivorous, preying on other creatures, and cannot therefore exist in such quantities upon a given area of ground as can for instance mussels, which live peaceably upon vegetable detritus. We have seen how, in our agriculture, the cultivation of vegetable products has given place to that of animal, and it is quite possible that we may in the future find the exploitation of our fisheries partly transferred from the carnivorous fish, to embrace in a far higher degree than at present the more productive elements such as those here referred to. In the course of the next few years, extensive experiments will be made in the Limfjord with a view to thus increasing the production of peaceable stock (oysters) by improvement of the bottom, and other methods. A great deal depends on how far this is found to succeed, and to what extent it is possible to carry out the experiment.

Much has thus been accomplished by the Station up to the present, but

more remains to be done. No one could have foreseen, a quarter of a century ago, what that period would being forth, nor is it easier now to predict what may be done in the future. The developement of science, however, in this as in so many other allied spheres, points ever forward towards higher and higher aims, and the number of biological stations throughout almost the whole of the globe has of late years enormously increased, despite the fact that many of them serve no practical, but often purely scientific ends.

The Station has maintained a constant communication with scientists and scientific institutions both at home and abroad, as is evidenced, *inter alia* by the considerable number of publications annually forwarded to the Station and its Director. Among Danish Institutions it will suffice to mention the Zoological Museum of the University with its scientists, who have in many ways afforded assistance in the execution of the work of the Station; assistance which is equally indispensable for the future continuance of the same. With the fishing population, the Station is on the friendliest footing; the exploitation by the State of the oyster monopoly has, quite recently, occasioned a slight local coolness in these amicable relations; it is hoped, however, that this will prove of but short duration. Both the Administration and the Parliament have, throughout the whole of the period herein described, evinced great interest in the Station, and furnished the means for continual extension of its work. The developement of the institution, albeit slow, has none the less been constantly progressive.

I July 1914.

(sd) **C. G. Joh. Petersen.**

List of principal publications directly connected with the work of the Biological Station.

C. G. Joh. Petersen: Om de skalbærende Molluskers Udbredningsforhold i de danske Have indenfor Skagen 1888. 8°. 162 pg. 2 Kort.

Det videnskabelige Udbytte af Kanonbaaden »Hauch«s Togter i de danske Have indenfor Skagen. 1893. 4°. 464 pg. Atlas in folio.

Contents: Echinodermata (Petersen), Diatomeer (Cleve), Undersøgelse af nogle Bundprøver (Rørdam), Mollusca (Petersen), Cephalopoda (Posselt), Crustacea malacostraca (Meinert), Hydrografi (Rørdam), Polyzoa (Levinsen), Ascidiæ simplices (Traustedt), Annulata, Hydroidæ, Anthozoa, Porifera (Levinsen), Nogle alm. Resultater (General Results. Engl.) (Petersen).

C. F. Drechsel: Oversigt over vore Saltvandsfiskerier med Kort og Planer. 1890. 4°, 10 pg. With Supplement: »Om Naturforholdene indenfor Skagen« af *C. G. Joh. Petersen.* Med Kort. 4°. 46 pg.

Fiskeri-Beretning for 1888—89, 89—90, 90—91, 91—92, 92—93, 93—94, 94—95, 95—96, 96—97, 97—98, 98—99, 99—1900, 1900—01, 1901—02, 1902—03, 1903—04, 1904—05, 1905—06, 1906—07, 1907—08. 1908—1913.

The Reports I—XXI of the Danish Biological Station are published in Danish in the corresponding „Fiskeri-Beretninger“, all save No. I being also published in English.

I. Fiskenes biologiske Forhold i Holbæk Fjord. 1890—91. 63 pg. Med et Kort.
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XXI. Valuation of the Sea, II. The animal communities of the sea bottom and their importance for marine zoogeography. 1913. (With 6 Plates, 3 Charts and an appendix.)

The Reports of the Biological Station are by *C. G. Joh. Petersen*, with the following exceptions:

Report XIII. *A. Otterstrøm.*
— XIV, II. *K. J. Gemzøe.*
— XVI. *C. H. Ostenfeld.*
— XX. *Petersen* and *Boysen Jensen*, and shorter papers by other writers.

Appendix to Report XXI

from

The Danish Biological Station.

1914.

Copenhagen.
Centraltrykkeriet.
1915.

Notes to Charts I and II.

By C. G. Joh. Petersen.

Since the publication of Report XXI, wherein I brought to a temporary conclusion the description of animal communities of the sea bottom as found in Danish waters, based upon investigations made with the bottom-sampler, I have frequently considered the question as to how these communities might presumably be distributed in other waters. No investigations with the bottom-sampler have been made outside Denmark, and the regularly distributed species of organisms which predominate either in point of weight or of numbers, or both, i. e., the characteristic species, have thus only been determined here. On looking through the lists of fauna, however, from other seas, as given in the extant works upon the subject, sometimes with notes as to which species are found together (more often without) and occasionally with remarks as to the frequency of one or another species, I formed an idea that very similar communities to those which I had discovered in Denmark occurred in far distant waters, with the same characteristic species, and, naturally, a greater or lesser number of other accompanying species.

In the Chart here I have endeavoured to sketch very roughly the distribution of these supposed communities outside the Danish waters, partly as mentioned above, according to the lists of species published, partly on the basis of descriptions of dredgings and trawl catches, and partly from Chart II here given, compiled by Dr. phil. J. N. Nielsen, showing the conditions of temperature on the sea bottom. Finally, I have utilised, where possible, such information as is furnished by the navigating charts concerning the nature of the bottom. In publishing Chart I, despite the inaccuracy which will doubtless be found to exist in its details, I do so with the object of furnishing a rough outline which may be corrected from time to time, as quantitative investigations come in from other countries; the chart is merely intended to serve as a graphical working hypothesis for such investigations.

Lists of species without information as to the quantitative occurrence of the various species are not sufficient for this purpose; nor are collections of material in which all, or at least several communities are mixed together, despite the fact that they exist separately in the sea. In making a comparison between

the animal life of various portions of the globe, it is indispensable, if any thorough knowledge of the subject is to be obtained, to compare each community with the same or corresponding community elsewhere, and not with one entirely different. It is necessary, therefore, to know these various communities, to keep them separate, and gradually to note them in a detailed survey.

Chart I shows how communities of widely different character may be found in close proximity one to another, especially on a highly indented coast line, where the fjord formation produces very heterogenous conditions, not only as regards nature of bottom, but also in respect of temperature, salinity, etc. Thus we find, in certain of the deep Norwegian fjords, no less than 5 different animal communities.

As the basis for this preliminary survey I have taken the animal communities of the level sea bottom; sand, mud or clay, entirely disregarding the epifauna as found on rocks, stones, or plants, which would demand a far greater knowledge of detail. I have also ignored various subdivisions of the communities in question as known to me from Danish waters, keeping to the main communites composed as follows:

I. **The Macoma Baltica community,** with
Macoma baltica,
Mya arenaria,
Cardium edule,
Arenicola marina etc. as the most evenly distributed characteristic species.

II. **The Venus communities,** with *Spatangidae,* found mainly on sandy bottom.
a) *Echinocardium cordatum,*
Venus gallina,
Tellina fabula,
Mactra subtruncata
in shallower water.
b) *Spatangus purpureus,*
Echinocardium flavescens,
Abra prismatica,
Psammobia faerøensis,
Mactra elliptica etc.
in deeper water.
Cyprina islandica is frequently found as an attendant species in both a) and b). *Venus* communities which have not yet been subjected to valuation may doubtless be found in still deeper water, together with *Spatangus Raschii* etc.

III. **The Brissopsis community,** on soft clay bottom, with
Brissopsis lyrifera,
Amphiura Chiajei,
Calocaris M'Andreae,

Nucula sulcata,
Eumenia crassa etc.

IV. **Communities from deeper water than the Brissopsis,** not yet subjected to valuation, but presumably on soft clay bottom, with
Pecten vitreus,
Abra longicallis, and various other species as characteristic types, or at least as important attendant species. — Future investigations will doubtless reveal the necessity of further subdivision here, and possibly a revised classification *(Amphilepsis norwegica).*

All these animal communities I—IV extend southward at least as far as France, where they in shallower water doubtless give place to the communities of the Lucitanian region, and northward to the northern Norwegian waters; they can, I think, be placed in opposition to all the communities of the areas marked green upon the chart, these having a far more northerly distribution; some indeed belonging indisputably to the higher arctic latitudes.

V. These **northern communities** I have never valuated, unless the Danish *Macoma calcarea* and *Astarte borealis* communities may be taken as belonging thereto. There is good reason for believing this to be the case; I have therefore coloured them green accordingly. I have made no attempt to define communities within the green northern areas, save for the fact that the deepest part of the Norwegian Sea is noted as a habitat of *Pecten frigidus* Vb., and the coastal regions of the extreme Arctic as that of *Yoldia arctica* Va.

The green areas doubtless contain other characteristic communities. I make no attempt at conjecture here; it may, however, safely be said that species such as *Astarte borealis, Banksii, crenata,* etc., *Macoma calcarea, moesta, Torelli, Loveni, Leda pernula* and *minuta, Nucula tenuis* and various others, besides echinoderms and other organisms, will be found to form part of or characterise these.

VI. **The communities of the Lucitanian Region** I know even less than the arctic, and am equally ignorant as to their distribution; they are therefore only indicated on the chart as a whole. I presume that their influence extends somewhat sparsely up along the western coasts of the British Isles and may perhaps even be noted as far as the northern coast of the Shetlands, faintly reappearing again off Bergen, where *Tapes decussatus* and others are found in shallow water at certain sheltered spots.

VII. As regard the **bottom fauna of the Atlantic** I am unable to note any evenly distributed, characteristic species. —

In drawing up Chart I, I have, as already mentioned, only considered the communities of the level bottom, not the epifauna. It will here suffice to mention that the epifauna of I, the *Macoma* community, is of so varied a nature, and has been so frequently described, that it need not be specially discussed in this connection. The appearance of *Haliotis* on the rocky coasts of France is here taken as approximately marking the northern limit of the Lucitanian communities. The epifauna found in II, the *Venus* communities, doubtless consists especially of *Modiola modiolus,* with *Ophiopholis aculeata, Alcyonium digitatum,* etc. The *Venus* communities often extend, on coasts facing the open sea, far down into deep water, their epifauna doubtless following suit. The common epifauna in

deep water will doubtless comprise the deep-sea corals, *Lophohelia* etc. frequently accompanied by *Pecten vitreus, Terebratulidae, Lima sp.*, etc.

Many attempts have been made to group the areas of occurrence of the individual species within geographical regions marked out on the basis of some few more or less known physical conditions such as temperature, salinity, etc., and some kind of survey has also been thus obtained. I am, however, inclined to believe that it would be more correct to take the actual distribution of the various species as a foundation for the study of descriptive zoogeography, according to the method pursued by several scientists, especially here in the North. The number of species being so enormously great, we can either select some few species having qualities which may be considered as particularly suitable, or we can keep, as I have done, to such species as are of quantitative importance, and of determining influence in formation, together with such communities as they constitute. In the case of the arctic regions I have not, owing to lack of material, been able to follow this principle throughout, but have supplemented the survey by the aid of two separate species, viz; for the deep waters of the Norwegian Sea, *Pecten frigidus*, and for the shallower areas of the extreme arctic region, *Yoldia arctica;* both according to the investigations of Ad. S. Jensen.

With regard to the further classification of animal communities in Denmark, the reader may refer to the Report of the Biological Station XXI, 1913. It should here be pointed out that the chart is not intended to show the full distribution[1]) of the separate characteristic species, but only that of the communities which are more or less distinctly characterised by these.

I venture to make this attempt, well knowing how imperfect it must be, because it will have to be made sooner or later, and the sooner it is made, the sooner, I trust, will it be repeated to better effect.

It will be seen from the chart, that all the communities shown in green are distributed throughout the so-called arctic region, but that occasional occurrences of arctic communities are noted in several of the fjords on the west coasts of Norway and Sweden; even farther down in the Danish Belts and in the Baltic we find arctic species occupying a characteristic position in shallow water.

The communities marked in red and yellow, and partly also those in blue, embrace the area known as the Boreal Region; the red *Macoma baltica* community however, has in particular very erratic tendencies outside the Baltic, extending from the Murman Coast to the north of France, where it is probably dissolved, some of its characteristic species, such as *Mya arenaria*, doubtless having their southern boundary here; it is here that we encounter the Lucitanian shore fauna. The yellow area should in all probability also end here on the coast, but is presumed to be continued in deeper water farther to the south. This last applies in an even greater degree to the pale blue area, which can doubtless be followed into the Mediterranean and down along the west coast of Africa, and does not therefore keep to the limits of the so called Boreal Area. The dark blue

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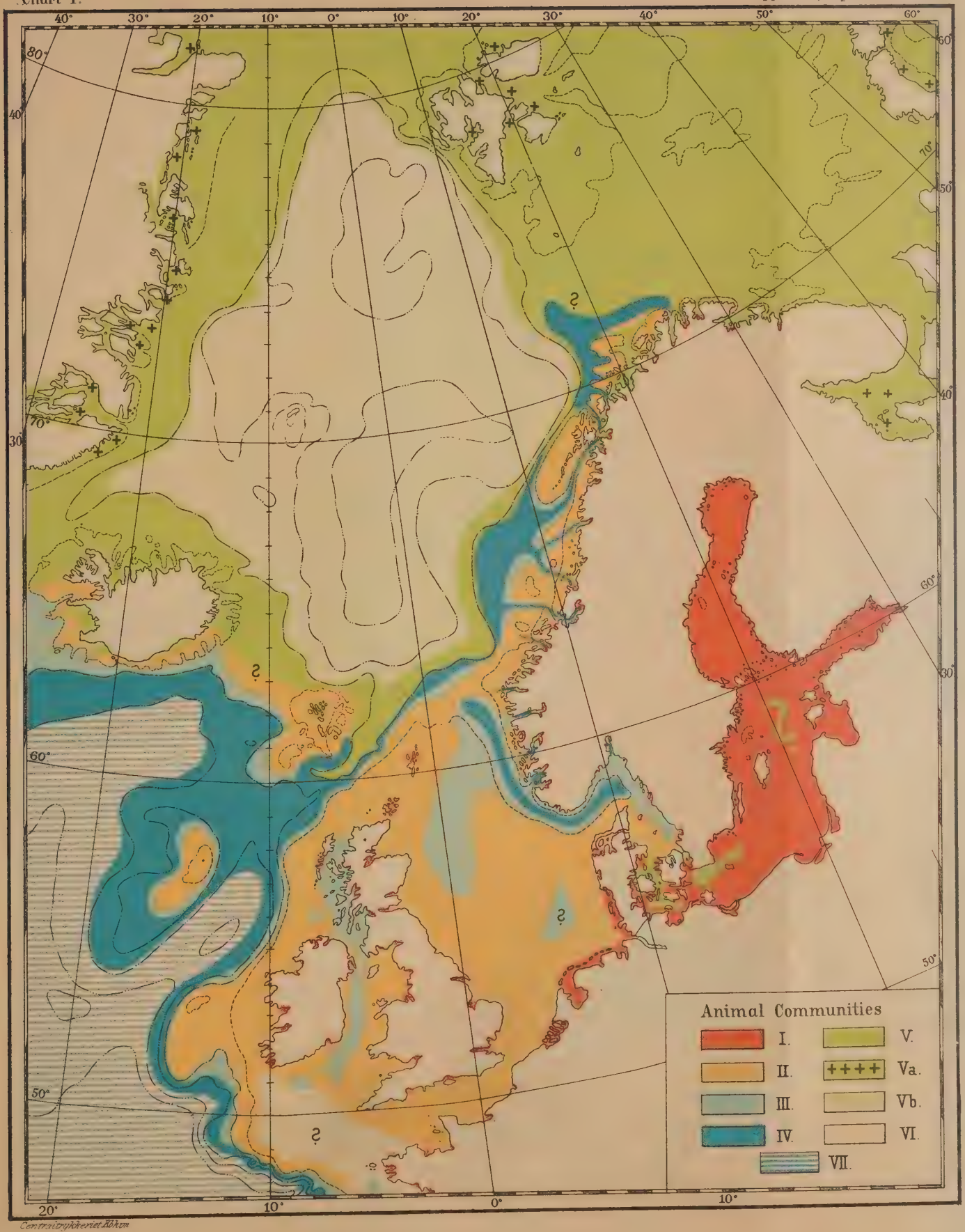
[1]) No attention has here been paid to the occurrence of young animals, or of single specimens, still less to shells of dead organisms, such being frequently found far outside the normal area of distribution of the species in question.

area doubtless extends still farther southward beyond the boreal boundary. The two blue areas are as a rule found in deeper water than the yellow and the red; probably, for this very reason, the species concerned will be able to penetrate farther to the south, where they will find, in the deeper water, conditions of temperature suited to their needs.

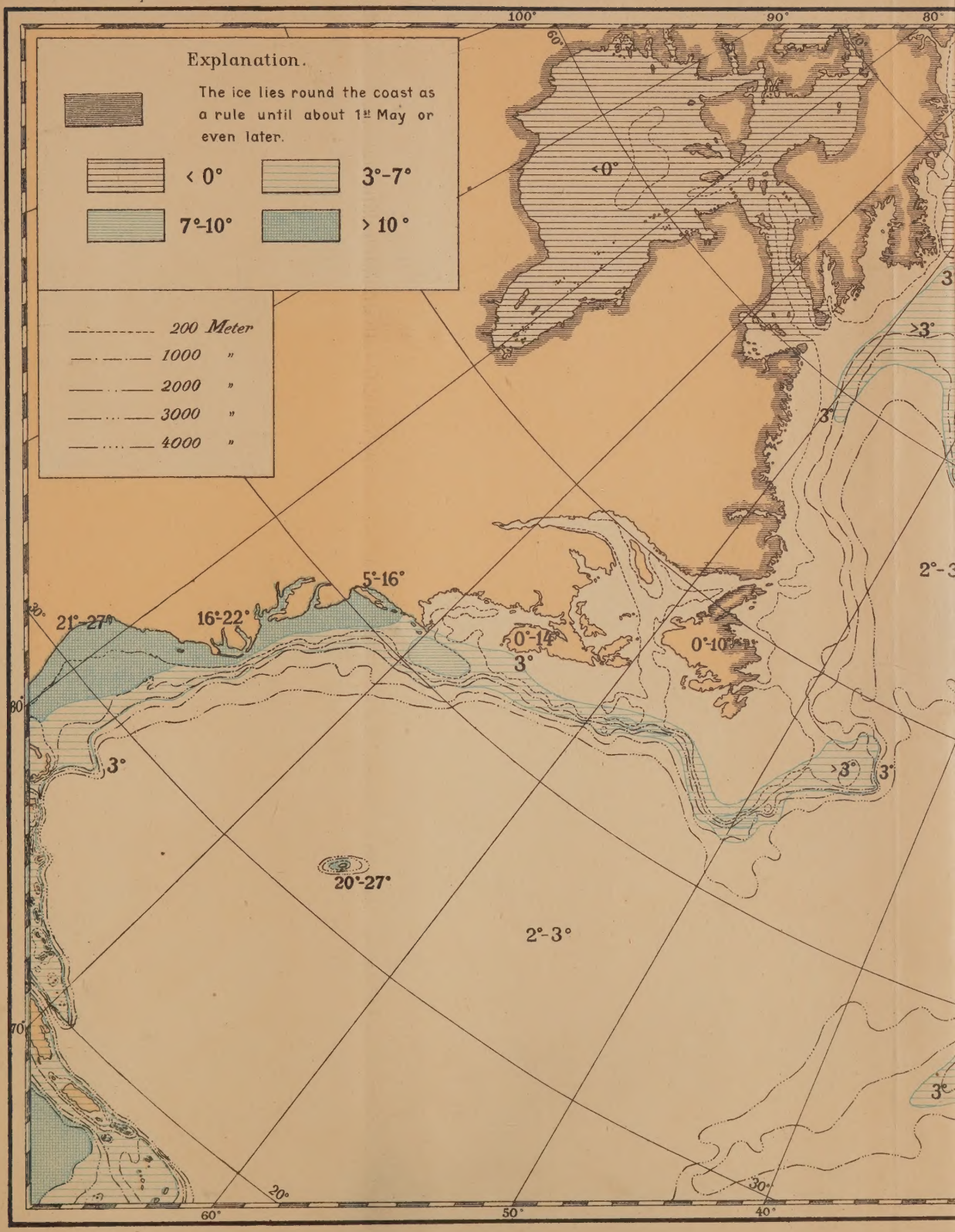
In order to describe the fauna of the Danish waters, and indeed, to obtain any survey at all, I have found it necessary to show that we have here to deal with different animal communities, each characteristically composed, and each with its own characteristic distribution. When once thus has been done elsewhere, the chart will probably have a very different appearance; the present one, however, which is only of a temporary nature, will then have served its turn.

With regard to Chart II, it should be mentioned, that while it is comparatively easy to roughly note the bottom temperature in the great seas, where it is almost constant, this is a far more difficult matter close in to shore, and in shellower waters, where the temperature is variable. The limits of oscillation of temperature as shown in the chart must therefore only be regarded as a rough guide, indicating the extremes of variations near the open coasts; in fjords and creeks, however, the limits of temperature are found to differ for places so closely adjacent as to render it impossible to mark them on a chart drawn to so small a scale.



Centraltrykkeriet Bhvn

Chart II. Temperature at bottom in Celsius.



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XXI. Valuation of the Sea. II. The animal communities of the sea bottom and their importance for marine zoogeography. 1913. (With 6 Plates, 3 Charts and an appendix.)

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Forfattede af *C. G. Joh. Petersen,* undtagen:

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